The Impacts of Contrasting Grazing Management on Biodiversity in Upland Calcareous Grasslands

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Contents

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Abstract

Calcareous grassland, considered among the most species rich and diverse habitats in Europe, underwent wide scale loss and degradation following post 1950s agricultural intensification. Consequently, they are the focus of conservation efforts and are protected in national and international legislation (e.g. EU Habitats Directive).

As elsewhere in Europe, a major cause of upland calcareous grassland loss and degradation in Britain was intensive grazing, typically with sheep. In recent years, conservation organisations have altered grazing practices in an attempt to prevent further loss and degradation by focussing management on conserving characteristic calcareous grassland vegetation. However, the impact of the contrasting grazing regimes used in this internationally important habitat on invertebrates is unknown.

This study is the first to investigate the impacts of a range of established grazing regimes (low intensity sheep grazing, low intensity cattle grazing, high intensity sheep grazing and no grazing) on aspects of plant diversity and structural complexity, carabid beetle diversity, and spider diversity in upland calcareous grasslands. It also provides the first evidence based management recommendations for UK upland calcareous grasslands which incorporate both plants and invertebrates. In addition, this study is also the first to assess the biodiversity value of acid grassland and limestone heath habitat patches that occur as

part of the calcareous grassland matrix and are not targeted by conservation management, by examining the spider fauna in each habitat in relation to calcareous grassland. Further evidence based recommendations for the management of these non-target habitats are made for the first time.

Key Words: Grazing; Carabid beetle; Spider; Management; Sheep; Cattle; Ungrazed; Vegetation structure; Calcareous; Heath.

Introduction

Conservation of Biodiversity

Biodiversity is fundamental to ecosystem functioning (Benton *et al.* 2003; Donald *et al.* 2006; Millennium Ecosystem Assessment 2005). However, over the last century increasing anthropogenic pressures including land use change, fragmentation and climate change have led to large scale biodiversity loss (Millennium Ecosystem Assessment 2005). Such loss leads to reduced ecosystem functioning e.g. nutrient recycling, pollination and resistance to invasion (Brook *et al.* 2008; Baillie *et al.* 2004; Larsen *et al.* 2005; Zavaleta and Hulvey 2004) which negatively impacts ecosystem services important to human well-being (Diaz *et al.* 2006; Millennium Ecosystem Assessment 2005). Recognition of this led to the development of international policy to halt biodiversity loss by protecting vulnerable species and habitats e.g. United Nations Convention on Biological Diversity and the European Commission Habitats Directive. Consequently, over 12% of the Earth's land surface is in nationally designated protected areas (UNEP-WCMC 2008), with the target of extending this to 17% by 2020 (UNEP-COP-CBD 2010). The largest coordinated protected area in the world, Natura 2000, covers 18% of land area in the European Union (European Commission 2016).

Many of the habitats in this protected area are a product of anthropogenic activities such as forest clearing, burning and grazing, which over the last 6000 years shaped the landscape into a patchwork of fragmented habitats which support high levels of biodiversity (Plieninger *et al*, 2006; Vorren 2010; Vos and Meeks, 1999). Consequently many of the protected areas are composed of inherently unstable semi-natural sub climax habitats, such

as semi-natural grassland and heathland, which require careful management to halt succession (Rook *et al.* 2004; Wallis de Vries *et al.* 2002).

Semi-natural Grasslands

Semi-natural grasslands are the remains of habitats created and maintained by low intensity farming practices, such as grazing and mowing, following woodland clearance, which began around 6000 years BP (Bullock *et al.* 2011; Eriksson *et al.* 2002; Green 1990) Although they are key areas for biodiversity in agricultural landscapes (Duelli and Obrist 2003; Zhao *et al.* 2015) they underwent extensive decline, degradation and fragmentation in the second half of the 20th century due to agricultural intensification and abandonment (Critchley *et al.* 2004; Duelli and Obrist 2003; Eriksson *et al.* 2002; van Dijk 1991; Wallis de Vries *et al.* 2002), which was driven by policy directed at maximizing food production (Common Agricultural Policy established in 1962) (Robinson and Sutherland 2002). Agricultural improvement of semi-natural grasslands through increased use of inorganic fertilisers, mechanisation and development of competitive strains of rye grass (*Lolium spp.*) resulted in the establishment of species poor plant communities dominated by a limited range of competitive species (Critchley *et al.* 2004; Ridding *et al.* 2015). Further areas of semi-natural grassland were lost due to conversion to arable land, abandonment and increased grazing intensity (Eriksson *et al.* 2002; Green 1990; Poschlod and Wallis de Vries 2002; Vickery *et al.* 2001). The extent of loss of semi-natural grassland across large parts of Europe in the 20th century was as much as 90% (Bernes 1994; Bullock *et al.* 2011). This loss is associated with declines in a range of taxonomic groups including birds, plants and invertebrates (Rich and Woodruff 1996; Vickery *et al.* 2001; Poschlod and Wallis de Vries 2002). In an attempt to prevent further loss, changes in agricultural policy have placed a greater emphasis on environmental benefits rather than maximising food

production (Dallimer *et al.* 2009) and agri-environmental schemes developed to promote the protection of biodiversity were introduced (Mouysset 2014). Many types of semi-natural grassland are now included in the Natura 2000 network of nature protection areas across Europe, which is comprised of Special Areas of Conservation, designated under the EC Directive on the Conservation of Natural Habitats and of Wild Flora and Fauna 1992 (92/43/EEC) (European Commission 2016) and Special Protection Areas, formulated under the EC Wild Birds Directive, 1979 (and now through Directive 2009/147/EC on the conservation of wild birds).

Grazing in Grasslands

Grazing has been fundamental in the development, maintenance and destruction of semi-natural grasslands across Europe (Bullock *et al.* 2011; Eriksson *et al.* 2002; Wallis de Vries *et al.* 2002). The transformation of forest to pasture around 6000 years BP was succeeded by enclosed low intensity farming which began around 2000 years BP (Bullock *et al.* 2011; Eriksson *et al.* 2002; Poschlod *et al.* 2005). This 'traditional' farming continued until the mid-19th century (Eriksson *et al.* 2002; Poschlod *et al.* 2005), the time at which highest phytodiversity occurred (Poschlod *et al.* 2005). Traditional farming was abandoned across Europe by the mid-20th century when agricultural intensification accelerated, resulting in low productivity grasslands often being 'improved' with the use of fertilisers to facilitate increasing livestock numbers, or they were abandoned resulting in succession to scrub and woodland (Critchley *et al.* 2004; Poschlod *et al.* 2005).

Grazing Impacts on Biodiversity

Grazing impacts plant communities in grasslands in a number of ways. At intermediate stocking levels the removal of plant biomass alters competitive relationships amongst plants which drives both heterogeneity within a landscape and preserves diversity (Bullock and Marriott, 2000; Rook *et al.* 2004; Scimone *et al.* 2007). Under high stocking densities the opposite is true and there is a decline in plant species richness and structural complexity (Deng *et al.* 2014; Komac *et al.* 2014). Further, under reduced or no grazing the above ground biomass of grass increases whilst that of forbs decreases (Deng *et al.* 2014), leading to diminished habitat quality and reduced species richness due to encroachment of dominant grasses and invasion of scrub (Jacquemyn *et al.* 2011; Komac *et al.* 2014; Wallis de Vries *et al.* 2002; Woodcock *et al.* 2005).

Dietary choice of livestock, determined by adaptations such as dental anatomy (Ferreira *et al.* 2013; Grant *et al.* 1985), also influences habitat heterogeneity, diversity and composition (Rook *et al.* 2004). Sheep display a higher degree of selectivity of forbs than cattle, which are more inclined to graze tall fibrous components than sheep (Reyneri *et al.* 1994; Grant *et al.* 1985). The avoidance of less palatable vegetation by sheep results in increased cover of less desirable grasses (Grant *et al.* 1985) whilst trampling by cattle can lead to increased levels of poaching (Betteridge *et al.* 1999).

In addition to impacts on vegetation, grazing also affects a wide range of non-plant taxa occupying all trophic levels e.g. birds, invertebrates and small mammals (Bell *et al.* 2001; Schmidt *et al.* 2005; Vickery *et al.* 2001; Woodcock *et al.* 2005). This occurs indirectly through its effects on plant community composition and plant architecture and directly through disturbance and provision of resources (Bell *et al.* 2001; Schmidt *et al.* 2005;

Vickery *et al.* 2001; Woodcock *et al.* 2005). For example, increased plant biomass as a result of reduced grazing intensity results in higher abundance of phytophagous insect species (Dennis *et al.* 1998; Dennis *et al.* 2008), intermediate grazing intensity supports greater field vole (*Microtus agresit* (Linneaus, 1761)) populations than more intense grazing (Schmidt *et al.* 2005), and higher intensity grazing is preferred to low intensity grazing by curlews (*Numenius arquata* (Linneaus, 1758)) (Tichit *et al.* 2005). Thus, management of semi-natural grasslands for conservation requires maintaining a careful balance of grazing intensity matched to the nature of the habitat and the conservation priorities, all of which benefit from increased knowledge of the organisms and responses involved.

Approaches to Grassland Conservation

The conservation of semi-natural grasslands is a central issue of nature conservation throughout Europe (Poschlod and Wallis de Vries, 2002). Given their dependence on, and sensitivity to disturbance, implementing appropriate management is vitally important for their conservation. This is particularly important given the contrasting responses of different species to different management (e.g. Dennis *et al.* 1998; Dennis *et al.* 2008; Schmidt *et al.* 2005; Swengel, 2001; Tichit *et al.* 2005). The two most common approaches to conservation management of semi-natural grasslands are grazing and mowing. Each approach aims to halt succession, suspending grassland in a sub-climax state through the removal of plant biomass to prevent dominance by one or few competitive species (Wallis de Vries *et al.* 2002; Tälle *et al.* 2016). By varying intensity, frequency, duration and timing, management can be fine-tuned to promote biodiversity (Littlewood *et al.* 2012; Watkinson and Ormerod, 2001). Such alterations in management can have different effects on vegetation species composition and structure and consequently on associated invertebrates (Littlewood *et al.* 2012; Catorci *et al.* 2014; van Klink *et al.* 2015). Grazing can gradually remove biomass through the growing

season which, together with deposition of dung and trampling, promotes structural heterogeneity in the sward (Tälle *et al.* 2016; Rook *et al.* 2004), providing greater potential for niche availability for invertebrates (Dennis *et al.* 1998; Morris, 2000). In contrast, the removal of plant biomass by mowing is sudden and creates homogeneity within the sward and can be catastrophic for several groups of invertebrates (Humbert *et al.* 2009; Johst *et al.* 2006). Both of these practices can be simultaneously beneficial and detrimental to different invertebrate taxa e.g. grazing benefits spiders but is detrimental to grasshoppers whilst mowing benefits grasshoppers but is detrimental to spiders (Tälle *et al.* 2016).

Owing to the contrasting responses of individual species and taxa to different management, monitoring of biodiversity beyond those targeted by changes in management is vitally important. Konvinka *et al.* (2008) highlighted the importance of monitoring following management changes in a study from the Czech Republic where conservation efforts were unable to conserve adequate areas of semi-natural grassland using traditional scythe-mowing. In an attempt to reverse successional processes and conserve larger areas, haymaking was reintroduced using modern practices of mechanically cutting large areas at once, which resulted in the local extinction of the endangered butterfly *Colias myrmidone* Esper, 1780. Though signs of the decline of *C. myrmidone* were reported, the push to restore botanical diversity took precedence. Indeed, the emphasis of management in semi-natural grasslands is typically placed on plants, with little consideration given to animals (van Wieren and Bakker, 1998; Wallis de Vries *et al.* 2002). Further, monitoring of conservation management treatments mostly refers only to vegetation, despite the importance of other taxonomic groups for the ecological functioning of grasslands (Poschlod and Wallis de Vries, 2002).

Invertebrates in Grasslands

In grasslands, invertebrates occupy a range of trophic levels and interact with all trophic levels, from primary producers to top predators (Prather *et al.* 2013). They also provide a wide range of important ecosystem services e.g. pollination, nutrient cycling, seed dispersal, decomposition, food web stability, disease regulation. They are directly and indirectly affected by management (Kruess and Tscharntke, 2002; van Klink *et al.* 2015; Veen *et al.* 2010). Foliar arthropod abundance can be depressed by large grazing herbivores due to competition for the same plant resources and inducement of defensive plant structures (Bailey and Whitham, 2003; Dennis *et al.* 2008; Zhu *et al.* 2012). In contrast grazing may facilitate insect diversity by increasing plant species richness and structural heterogeneity (Cagnolo *et al.* 2002; Joern, 2005; Zhu *et al.* 2012).

Their differential responses to changes in management and habitat conditions have resulted in invertebrates experiencing disproportionately high rates of decline in semi-natural grasslands across Europe (Bourn and Thomas, 2002; Thomas and Clarke, 2004). Their importance in ecosystem function, contrasting responses to management and rate of decline render understanding management impacts on invertebrates in semi-natural grassland both vitally important and timely. However, as Wallis de Vries *et al.* (2016) notes, grazing management still lacks a good evidence base, particularly for insect communities. But most importantly, invertebrates are just fascinating in their own right!

Spiders and Carabid Beetles in Grasslands

Spiders are among the most abundant animals in terrestrial ecosystems and occupy an important role in terrestrial food webs as both predators and prey (Turnbull, 1973; Uetz, 1991). Though exclusively predators, they encompass a wide range of foraging strategies and dispersal capabilities and as such are differentially sensitive to variations in vegetation architecture and disturbance (Barriga *et al.* 2010; Bell *et al.* 2001; Diehl *et al.* 2013; Gibson *et al.* 1992). They are known to respond to grassland management on a species, assemblage and feeding guild level (Bell *et al.* 2001; Dennis *et al.* 2015: Duffey, 1993). Their role as both predators and prey ensure that they provide important ecosystem services in grassland trophic functioning. Thus, their ecological requirements, functional roles and responses to disturbance make them an interesting group for studying differences in diversity among contrasting management and habitats.

Carabid beetles, on the other hand, though mostly predatory, occupy a range of trophic levels, as predators, scavengers, granivores, herbivores and omnivores (Larochelle, 1990; Lövei and Sunderland, 1996). Their functional roles as predators, granivores and prey provide important ecosystem services in grasslands through pest control, weed control and food provision for other taxa. They are sensitive to changes in habitat quality, particularly their weakly chitinised larvae which are intolerant of microclimate extremes (Kromp, 1999). Their habitat selection is influenced by microclimate e.g. temperature, light and humidity (Thiele, 1977). As such they are sensitive to responses of vegetation to management in grasslands (Woodcock *et al.* 2009, 2007). Coupled with their contribution to ecosystem services and sensitivity to changes in habitat quality, the substantial overall decline in Britain reported by Brooks *et al.* (2012) also highlights the importance of understanding their responses to management in grasslands.

Semi-Natural Grasslands in the British Uplands

Semi-natural grasslands in Britain are considered early successional habitats that require intervention to prevent succession to scrub or woodland (Ridding *et al.* 2015). It is estimated that 88% of semi-natural grassland in the UK occurs in the uplands, though just 1.4 % is designated as priority habitats which include calcareous grassland, hay meadows and purple moor grass & rush pastures (calculated from Bullock *et al.* 2011). The remaining 86% is semi-natural acid grassland which is often a product of overgrazing of heather moorland (Anderson and Yalden, 1981; Bullock *et al.* 2011), which declined by 36% in some areas during the 20th century (Anderson and Yalden, 1981). The decline of heather moorland and the subsequent increase of acid grassland coincides with a 26% increase in sheep numbers in the uplands, which peaked at an all-time high in the 1990s (Fuller and Gough, 1999). Increased grazing pressure during this time also coincided with the loss of priority semi-natural grasslands (Ridding *et al.* 2015).

Upland Calcareous Grassland

The exceptional diversity of plants and invertebrates in calcareous grassland renders them one of the most species rich and diverse habitats in Europe (Roesch *et al.* 2013; Wallis de Vries *et al.* 2002) and as such they are of great conservation concern (Poschlod and Wallis de Vries, 2002). However, they underwent large scale loss and degradation following post 1950s agricultural intensification due to changes in management practices, such as increased use of fertilisers, greater stocking densities and occasionally abandonment (Fischer and Stocklin, 1997; Poschlod *et al.* 2005; Roesch *et al.* 2013; Wallis de Vries *et al.* 2002). This resulted in a dramatic decline in plant and invertebrate species richness (Bourn and Thomas, 2002; Poschlod and Wallis de Vries, 2002). Consequently, they are included in Annex I of

the EU Habitats Directive, with an estimated 595 973 ha protected in the Natura 2000 network across EU member states (Calaciura & Spinelli, 2008).

In Britain, calcareous grassland did not escape agricultural intensification with high stocking densities of sheep implicated as a major cause of habitat deterioration and the decline of associated plants, invertebrates and birds in upland regions (Dennis *et al.* 2008; Fuller and Gough, 1999). Indeed, increased grazing pressure between the 1960s and 1990s coincided with the 37% loss of upland calcareous grassland in England between 1960 and 2013 (Ridding *et al.* 2015) which now covers just 0.1% (22000-25000ha) of total UK land cover (calculated from Maddock, 2008; DEFRA, 2013).

Upland calcareous grassland occurs on thin, well drained, lime rich soils found overlying limestone bedrocks interspersed with superficial deposits of glacial till or loess which results in a patchwork of a matrix of calcareous grassland, acid grassland and limestone heath (Rodwell, 1992; Rodwell *et al.* 2007; Joint Nature Conservation Committee, 2007). Conservation management of this upland grassland matrix is targeted at conserving the characteristic vegetation of the calcareous grassland, with little attention to patches of acid grassland or limestone heath, despite the latter's inclusion in Annex I of the EU Habitats Directive (Joint Nature Conservation Committee, 2013). Over the last 15 years conservation management has involved a reduction of stocking levels which typically involved a shift from grazing with high numbers of sheep to lower stocking densities of cattle. However, the impact of these changes in grazing management on biodiversity, both in calcareous grassland and the non-target habitats of acid grassland and limestone heath, has until now, been unknown.

Understanding the effects of these commonly used grazing regimes on a range of taxa is important to ensure that they are not detrimentally damaging, they are able to achieve conservation aims and to highlight the importance of non-plant taxa to overall biodiversity and functioning of this internationally important habitat.

Research Aims

The aims of this study were to assess the impacts of established (>10 years) grazing management regimes on plants, carabid beetles and spiders in upland calcareous grassland; to determine the biodiversity value of non-target habitats in the calcareous grassland matrix, using spiders as a model group; and to provide evidence based management recommendations for upland calcareous grassland and associated habitats, taking into account aspects of carabid beetle and spider diversity in relation to vegetation composition and structural complexity.

Thesis Outline

This thesis consists of three research papers which address one or more of the outlined research aims (Table 1). Chapter two examines the impacts of low intensity sheep grazing, low intensity cattle grazing and ungrazed regimes on aspects of plant and carabid beetle diversity and assesses whether these two groups respond in a similar way to grazing management. Chapter three examines the impacts of low intensity cattle grazing, low intensity sheep grazing, high intensity sheep grazing and ungrazed regimes on vegetation structural complexity and the subsequent impacts on aspects of spider diversity. Chapter four examines the spider species communities of acid grassland and limestone heath patches in relation to calcareous grassland under light sheep grazing. Chapter five draws upon the

previous chapters to provide a range of evidence based management recommendations for upland calcareous grassland and related habitats.

Table 1: Research aims addressed in each thesis chapter

Chapter/biodiversity approach	Grazing impacts	Value of non-target habitats	Management recommendations
2 – Plants and Carabid Beetle diversity	X		X
3 – Vegetation structure and spiders	X		X
4 – Spider diversity		X	X

Chapter 2

Impacts of contrasting conservation grazing management on plants and carabid beetles in upland calcareous grasslands

In press in *Agriculture, Ecosystems and Environment*

Abstract

Calcareous grassland is among the most species rich and diverse habitat in Europe, but has faced decline due to agricultural intensification and abandonment. In recent years, conservation organisations have changed grazing practices in this habitat in an attempt to maintain characteristic vegetation. However, there has been little consideration of the effects of changes in grazing practices on invertebrate communities or their relationship with plant communities. This study determines the impacts of commonly used grazing practices in internationally rare upland calcareous grasslands on vegetation and on carabid beetles, a diverse group that are known to respond to environmental change. Typical conservation management regimes (light cattle grazing, light sheep grazing and ungrazed), established for over ten years, were examined in three regions of Britain. Carabid beetles were sampled using pitfall traps from late April – early September 2013 and per cent cover of plant species was recorded in 2m x 2m quadrats paired with pitfall traps sequentially throughout the sample period. Plant and beetle species composition differed significantly between regimes, as did plant species richness where ungrazed sites had significantly fewer species than sheep or cattle grazed sites. In contrast, beetle species richness did not differ by grazing type. Three beetle species were significantly associated with grazing management regimes: *Carabus arvensis* with light cattle grazing, and *Carabus violaceaus* and *Synchus vivalis* with light sheep grazing, the former two having undergone major population declines in the UK. Grazing regime affects both plant and carabid beetle communities and is important in supporting distinct species compositions as well as rare and declining species. Carabid beetles did not always respond in the same way as plants to grazing regime, suggesting that conservation managers should exercise caution when using

plant species composition or broad measures of plant diversity to indicate biodiversity value, identify priority habitats or select grazing regimes to support a particular habitat condition.

Key words: Community, Carabid beetle, Livestock, Ungrazed, Upland, Vegetation.

Introduction

Calcareous grassland is one of the most species rich and diverse habitats in Europe (Wallis de Vries *et al.* 2002). Their exceptional diversity of plants and invertebrates render them of great conservation interest (Boschi and Baur, 2007; Krauss *et al.* 2003; van Swaay, 2002; Wallis de Vries *et al.* 2002). In Europe, large areas have been lost since the 1950s due to changes in management practices, such as increased use of fertilisers, greater stocking densities and occasionally abandonment (Fischer and Stocklin, 1997; Poschlod *et al.* 2005; Roesch *et al.* 2013; Wallis de Vries *et al.* 2002). This has resulted in a dramatic decline in plant species richness (Poschlod and Wallis de Vries, 2002). Consequently, calcareous grassland is now protected in national and international legislation (e.g. EU Habitats Directive).

Semi-natural grasslands are sub-climax communities that require intervention to prevent succession to scrub or woodland (Rook *et al.* 2004) and to maintain plant diversity (Roesch *et al.* 2013; Wallis de Vries *et al.* 2002). Grazing is commonly used as a conservation tool for maintaining diversity within these plant communities. Through grazing the removal of plant biomass alters competitive relationships amongst plants which drives both heterogeneity within a landscape and preserves diversity (Bullock and Marriott, 2000; Rook *et al.* 2004; Scimone *et al.* 2007). Dietary choice of livestock, determined by adaptations such as dental anatomy (Ferreira *et al.* 2013), is the principle factor influencing habitat heterogeneity, diversity and composition (Rook *et al.* 2004). For instance, sheep exhibit more selectivity in their diet than cattle, resulting in increased cover of less desirable grasses (Grant *et al.* 1985). Additionally, the intensity of grazing also impacts upon vegetation, as suggested by the intermediate grazing optimisation model (Grime,

1973), with high stocking densities or abandonment resulting in a decline in plant species richness and structural complexity, whilst moderate stocking densities lead to increased plant species richness (Deng *et al.* 2014: Grime, 1973; Vickery *et al.* 2001). Further, at low densities, the above ground biomass of grass increases whilst that of forbs decreases (Deng *et al.* 2014); the resulting encroachment of dominant grasses reduces species richness and the increased litter deposition results in eutrophication (Calaciura and Spinelli, 2008; Jacquemyn *et al.* 2011; Wallis de Vries *et al.* 2002; Woodcock *et al.* 2005).

Selection of grazing regime has implications for invertebrate communities directly through disturbance or provision of resources, such as dung or carrion, and indirectly through its effects on plant species composition, plant architecture and heterogeneity (Dennis *et al.* 2001; Morris 2000; Vickery *et al.* 2001; Woodcock *et al.* 2005). The *habitat heterogeneity hypothesis* predicts that the greater the heterogeneity of a habitat the more species can coexist in that habitat (Pianka 1966). Thus, it follows that under grazing conditions that produce a more heterogeneous sward, such as low intensity grazing with cattle or sheep compared to no grazing, invertebrate species richness will be enhanced as there is greater niche availability.

There are currently an estimated 595 973 ha of calcareous grassland within Europe, of which around 33 419 ha is in the United Kingdom (Calaciura and Spinelli, 2008) and an estimated 60 – 75 per cent of this occurs in the British uplands (Maddock, 2008). As elsewhere in Europe, upland areas within Britain experienced decline in this habitat due to intensive grazing, typically with sheep (Dennis *et al.* 2008; Fuller and Gough, 1999). Indeed, between 1990 and 1998 there was an 18% decline in calcareous grassland in the UK (Haines-Young *et al.* 2000). To conserve the characteristic vegetation of this habitat

there has been a reduction in stocking levels within the last decade. This typically involves a shift from grazing with high numbers of sheep to a lower stocking density of cattle, though occasionally lower stocking densities of sheep or no grazing occurs. These so-called 'conservation grazing regimes' are based on suggested appropriate annual stocking rates of 0.25 LU ha^{-1} yr^{-1} for maintaining biodiversity (Backshall *et al.* 2001). However, there have been few studies which address the impact of these established low stocking conservation grazing regimes and compare ungrazed regimes, on plants and fewer still on invertebrates in these internationally important habitats (Wallis de Vries *et al.* 2002, 2016). Previous studies of grazing impacts on calcareous grassland have examined small experimental plots (e.g. Barbaro *et al.* 2001; Woodcock *et al.* 2005; Jacquemyn *et al.* 2011). The present study is the first to present an evidence base for the impacts of established (>10 years) conservation grazing management on biodiversity in upland calcareous grasslands, using plants and carabid beetles as models. This study aims to determine the impact of low intensity sheep grazing, low intensity cattle grazing and ungrazed regimes on plant and carabid beetle communities and tests the following hypotheses:

1. In low intensity conservation grazing regimes with either cattle or sheep, there will be greater plant species richness compared to ungrazed regimes.

   This follows the intermediate grazing optimisation model where plant species richness reaches a maximum at intermediate biomass as a product of optimum grazing levels (Grime, 1973). According to this model, species richness will increase or decrease depending on grazing intensity, since this directly alters the amount of biomass and hence alters competition. It is expected that even below recommended optimum stocking levels, low intensity cattle or sheep grazing will

lead to greater plant species richness compared to ungrazed regimes as a consequence of reduced biomass.

Supplementary to hypothesis one, it is expected that owing to equal stocking densities, plant species richness will not differ between low intensity cattle and sheep grazing regimes.

2. It is further expected that in line with plant species richness, and following the *habitat heterogeneity* hypothesis, there will be greater carabid beetle species richness in low intensity conservation grazing regimes with either cattle or sheep than ungrazed regimes.

   Supplementary to hypothesis two, it is expected that due to the disturbance action of grazing livestock, greater habitat heterogeneity in grazed compared to ungrazed regimes will result in a greater range of food resources available through seeds or prey, thus providing a greater range of niches for more carabid beetle species to occur. Again, it is expected that due to comparable stocking densities, no difference in carabid beetle species richness will be observed between sheep and cattle regimes.

3. There will a distinct species composition among the three grazing types for both plants and carabid beetles due to the different grazing actions of cattle and sheep, as discussed above, even at low intensities.

Plants are directly impacted by grazing and are the target of conservation efforts. Conversely, invertebrates are very rarely considered when grazing management decisions are made for upland calcareous grassland, despite their importance for the functioning of ecosystems. Carabid beetles, for instance, play an important role in grasslands through their roles such as predators, as granivores and as a food source for other animals (Lövei and Sunderland, 1996) yet are overlooked in management decisions. Management is typically focused on maintaining particular plant communities and condition of sites is always assessed based on vegetation characteristics. Results from this study, weighed against other evidence, will inform management recommendations for enhancing biodiversity through grazing regimes in rare calcareous grasslands and determine whether plant species composition can be used to indicate carabid beetle species composition, a useful tool in the context of conservation management in these habitats.

Methods

Study Sites

Three grazing types were selected for study within the most extensive upland limestone areas within the UK: ungrazed, cattle grazed and sheep grazed regimes (with a negligible number of cattle (<0.02 Livestock Units per Hectare per Year (LU ha^{-1} yr^{-1})) and herein referred to as sheep grazed). The current grazing regime had been in place for at least ten years prior to investigation across all locations. Grazed regimes were deemed as being lightly grazed for upland calcareous grassland as they had a grazing intensity of less than 0.24 LU ha^{-1} yr^{-1} (Backshall *et al.* 2001) calculated as: Annual Equivalent Stocking Density = ((N*GLU/H)*(M/12).

Where: N = Number of individuals, GLU = Grazing Livestock Unit (taken from Nix, 2004), H = Hectares and M = Number of months grazed. Detail of stocking densities and duration of grazing is provided in table 1.

Each grazing regime was replicated across three geographically distinct regions separated by 20-37km in Northern England (54°29′18.55″N, 002°32′33.00″W) (54°11′43.30″N, 002°21′00.13″W) (54°06′29.41″N, 002°03′55.04″W) (Fig. 1). In each region three extensive areas of limestone grassland (size 15 ha – 525.68 ha, median 82.75) were selected within which three sampling locations were established. These were separated by a minimum of 150m (median 330m) to ensure statistical independence of samples (Digweed *et al.* 1995), and a minimum of 50m from the edge and away from disturbance e.g. footpaths, water troughs etc. Spatial independence of samples was confirmed with Moran's I based on nearest neighbour distances for all 27 locations for carabid beetle

abundance, showing there was no significant spatial autocorrelation (Moran's I ± SD: 0.02 ± 1.47, p = 0.07) (Bivand *et al.*, 2014).

In each of the three regions there were three gazing types giving a total of 27 areas selected for study (three replicates per grazing type nested within region). Elevation ranged from 288 – 396m, median 335m. Soil across the sites was generally base rich with some deposits of glacial till and peat.

All areas were characterised by a mix of calcareous grassland, upland heath and limestone pavement, and were surrounded by a mix of extensively and intensively grazed open grassland. Typical areas of calcareous grassland were selected for study through the use of detailed habitat maps and aerial photographs. Within each location, surveys of vascular plants, bryophytes and epigeaic carabid beetles were conducted between April – September 2013.

Table 1 Annual stocking intensities and duration of grazing for each grazing regime within each region.

Site	Livestock Type	Grazing Intensity ($LU/ha^{-1}/yr^{-1}$)	Duration of Grazing (months)
Region 1	Cattle	0.18	6
Region 2	Cattle	0.13	5
Region 3	Cattle	0.19	10
Region 1	Sheep	0.10	12
Region 2	Sheep	0.12	12
Region 3	Sheep	0.15	5

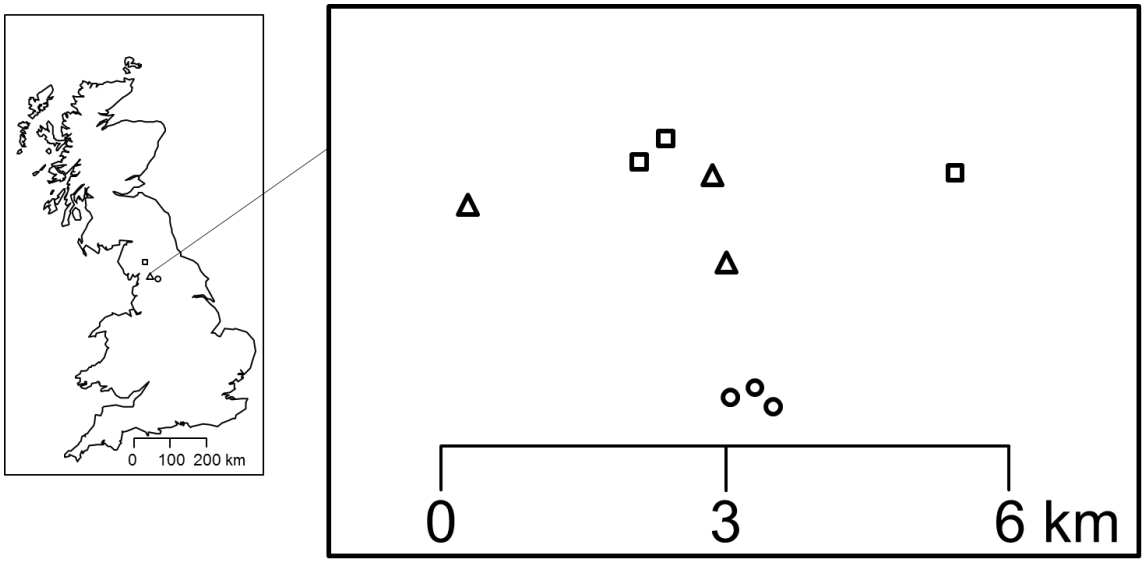

Figure 1 Map displaying the location of the three sample regions within mainland Britain. The highlighted box displays the sample sites within one sample region. Sample site locations within the two other regions are comparable to the one highlighted here. Grazing types are identified as: triangles = cattle, squares = sheep, circles = ungrazed.

Vegetation Sampling

To incorporate changes in plant communities across the sampling period one 2m x 2m quadrat was recorded at each sampling location at approximately three weekly intervals to achieve a total of six quadrats per sample location for the duration of the sampling season, between 27th May 2013 and 20th September 2013. For three of the sample locations in the sheep grazed regime permission was restricted for the first two sampling rounds, so two quadrats were recorded in each of the final two rounds of sampling to ensure the same sampling effort. Per cent cover of all vascular plants and bryophytes was estimated to the nearest five per cent. Vascular plants were identified to species using Poland and Clement (2009) and Rose (2006) and bryophytes identified using Smith (2004). Nomenclature follows Stace (2010) for vascular plants and Smith (2004) for bryophytes.

Invertebrate Sampling

Within each sampling location a line of six pitfall traps, spaced 2m apart and 1m from vegetation quadrats, was set up to capture carabid beetles (Gardner *et al.* 1997; Haysom *et al.* 2004; Oxbrough *et al.* 2012). The sixth trap was kept as a spare in case of loss or damage. Each trap consisted of a plastic cup approximately 7cm in diameter and 9cm deep and was covered with a square plastic lid suspended 1cm from the ground by pegs to prevent flooding. 1cm depth of ethylene glycol was used in traps as a killing and preserving agent. To prevent traps being trampled or interfered with by livestock, in grazed areas each trap was protected by a secured cage made from 2.5cm x 2.5cm gauge mesh. These cages do not affect the trapping rates of ground-dwelling invertebrates (Oxbrough *et al.*, 2012). In all but one grazing regime at one region, traps were set between 29/04/2013 and 04/09/2013 and were changed every 21 days, giving a total of 127 trap days. Due to restrictions in permission to sample in one of the sheep grazed regimes traps were set from

01/07/2013 and 02/09/2013 in this site, giving a total of 64 trap days. Samples from five of the traps within each location were pooled for analysis, with the sixth kept as a spare in case of trap loss.

Pitfall traps are a widely used sampling method to catch active ground dwelling invertebrates in grasslands and heathlands (Gardner *et al.* 1997; Haysom *et al.* 2004). They do not provide measures of absolute abundance, but rather a relative count based on a species' density and activity (Greenslade, 1964) and are less likely to capture species that are more sedentary. Nevertheless, their high catch rate and ease of setting up render their use appropriate in large scale studies with multiple sites (e.g. Oxbrough *et al.* 2012; Taboada *et al.* 2010). Species identification and nomenclature follows Luff (2007). Carabid beetle reference specimens are housed at the Edge Hill University Department of Biology arthropod collection.

Data Analysis

For vegetation, per cent cover data collected at each sampling location for the duration of the sampling period was averaged, giving a single measurement of vegetation cover from the six quadrats recorded at each location. For carabid beetles, the five traps in each sampling location were pooled across the full sampling period. To account for differences in trapping effort all samples were standardised by trap day by calculating the abundance of each species at each location and dividing it by the number of actual trap days at that location and then multiplying it by the maximum number of trap days across all locations (127), a standard method used in studies using pitfall trapping (Bergeron *et al.* 2013; Blanchet *et al.* 2013: Pinzon *et al.* 2013).

Statistical analyses were carried out with R statistical software (version 3.2.0.) (R Core team, 2015) and EstimateS (version 9.1.0) (Colwell, 2013).

To address hypothesis one species richness was calculated for vegetation across all grazing regimes using the specnumber function in the vegan package (Oksanen *et al.* 2015) in R. Generalised Linear Mixed Models (GLMM) were performed with Poisson errors to analyse the differences of grazing regime (cattle, sheep and ungrazed) on vegetation species richness with the glmer function of the lme4 package (Bates *et al.* 2015). Grazing regime was modelled as a fixed factor with region modelled as a random factor. The model was tested for over dispersion of Poisson errors and was found to be under dispersed (vegetation = 0.68). To correct for under dispersion individual level variability was included as a random variable. Results indicated that the individual level variable did not account for any variance and as such was omitted from the final model. Tukey pairwise comparisons were used to test for differences among grazing regimes, correcting p values for multiple comparisons with the Holm method using the ghlt function of the multcomp package (Hothorn *et al.* 2008). To determine if plant per cent cover or vegetation height were different among grazing regimes GLMMs were again performed using the method described above, to compare the proportion of cover that was grass among grazing regimes a GLMM was performed with Binomial errors and over dispersion dealt with as above (Crawley, 2012).

To address hypothesis two, differences in carabid beetle species richness were examined with raw species data (not standardised by trap day) using sample based rarefaction calculated using EstimateS, version 9.1.0 (Colwell, 2013) with rarefaction curves produced in R and scaled by the number of individuals. This technique accounts for differences in

sampling effort by standardising species richness for the number of individuals within a sample. Rarefaction estimates the number of species expected in a random sub-sample extracted from a larger sample (Chao, 2005; Magurran, 1988, 2004). Indicator species analysis (Dufrene and Legendre, 1997) was used on both taxon groups to determine species that were strongly associated (both common and frequent) with each grazing regime using the indval function of the labdsv package (Roberts, 2015). Indicator Species Analysis produces indicator values between 0 – 1, a value of 1 represents a perfect indicator that is always present in a particular treatment and is exclusive to that treatment (McCune *et al.* 2002). Significance of indicator values was assessed using a Monte Carlo randomisation procedure with 4999 iterations. Significant indicator values infer species associations with each grazing regime as a mechanism to characterise habitat use by plants and carabid beetles.

To address hypothesis three Principal Components Analysis was computed on Hellinger transformed species data using the RDA function in the vegan package in R. Region was included as a covariable and its effects removed from the community matrix with the residuals submitted to the next stage. Ordinarily this would produce a partial redundancy analysis but as the constraining variable 'grazing' was omitted the model produced a Principal Components Analysis for which the effects of region were partialled out. To determine differences in plant or carabid beetle species compositions between grazing types Permutational Multivariate Analysis of Variance (PERMANOVA) was used with 9999 permutations using the adonis function of the vegan package. Differences in multivariate dispersion among groups was explored using between grazing regime beta diversity results with the Anova function of the Car package (Fox and Weisberg, 2011) as

PERMANOVA is sensitive to these differences. Results of this are only discussed where significant.

To determine if plant species composition can be used as a tool in conservation management to indicate carabid beetle species composition, similarities in community composition between plants and carabid beetles were explored using the Procrustes rotation method (Jackson, 1995: Peres-Neto and Jackson, 2001) with the protest function in the vegan package. This measures concordance between two matrices by subjecting one matrix to reflection, rotation, translation and dilation in order to minimise the sum of squared residuals between observations in the original matrix and the identical observations in the target matrix (Jackson, 1995). PCA axes one and two scores of both groups (plants and carabid beetles) were best fitted to find a suitable superimposition using the protest function in vegan which uses randomisation tests to assess the statistical significance of concordance between matrices (Jackson, 1995). Using a correlation like statistic, comparable to Pearson correlation r^2 (Peres-Neto and Jackson, 2001), Protest produces a correlation value between 0 and 1, with larger values indicating better concordance. To determine if there were any differences in concordance amongst grazing regimes coordinates for both vegetation and carabid beetle points were taken from a procrustean superimposition plot and distance between points was calculated using Pythagorean Theorem and significance analysed using analysis of variance using the aov function. The relationship between plant species richness and carabid beetle species richness was also examined using Spearmen's rho correlation using the cor.test function in the Hmisc package (Harrell, 2015).

Results

A total of 102 plant species were recorded, (79 species of vascular plants and 22 species of bryophytes). 54.1% of total plant abundance was made up by two species; *Sesleria caerulea* (37.3%) and *Festuca ovina* (16.8%). These were the only species that individually made up more than 10% of total plant abundance. A total of 5866 individual carabid beetles from 23 species were collected. Taken across all locations two species made up 80.2% of the total abundance of individuals; *Pterostichus madidus* (69.3%) and *Pterostichus melanarius* (10.9%). A full list of species is given in Appendix A1.

Plant and carabid beetle species diversity among grazing regimes

Plant species richness was significantly different among grazing regimes ($X^2_{(2, N = 27)}$ = 14.03, p<0.001) being greater in both cattle grazed and sheep grazed than ungrazed locations (z = -3.24, p<0.01; z = -3.39, p<0.01 respectively) (Fig. 2a). Total plant per cent cover was significantly different ($X^2_{(2, N = 27)}$ = 11.57, p<0.01) and was driven by the greater cover in cattle grazed compared to ungrazed (z = -3.38, p<0.01) (Fig. 2b). Further, the proportion of cover of grasses was significantly different among grazing regimes ($X^2_{(2, N = 27)}$ = 59.61, p<0.01), with greater cover in ungrazed than either cattle grazed or sheep grazed (z = 7.42, p<0.01, z = 2.40, p<0.05 respectively) and greater cover in sheep grazed than cattle grazed (z = 5.11, p<0.01) (Fig. 2c). Vegetation height was significantly different among grazing regimes ($X^2_{(2, N = 27)}$ = 19.62, p<0.001), with the difference greatest between cattle grazed and ungrazed (z = 4.34, p<0.01), sheep grazed and ungrazed (z = 2.48, p<0.05) and marginally significant between cattle grazed and sheep grazed (z = 1.98, p=0.05) (Fig. 2d).

For carabid beetles, rarefaction curves indicated that species richness did not differ among grazing regimes (Fig. 3), as indicated by the overlap in confidence intervals.

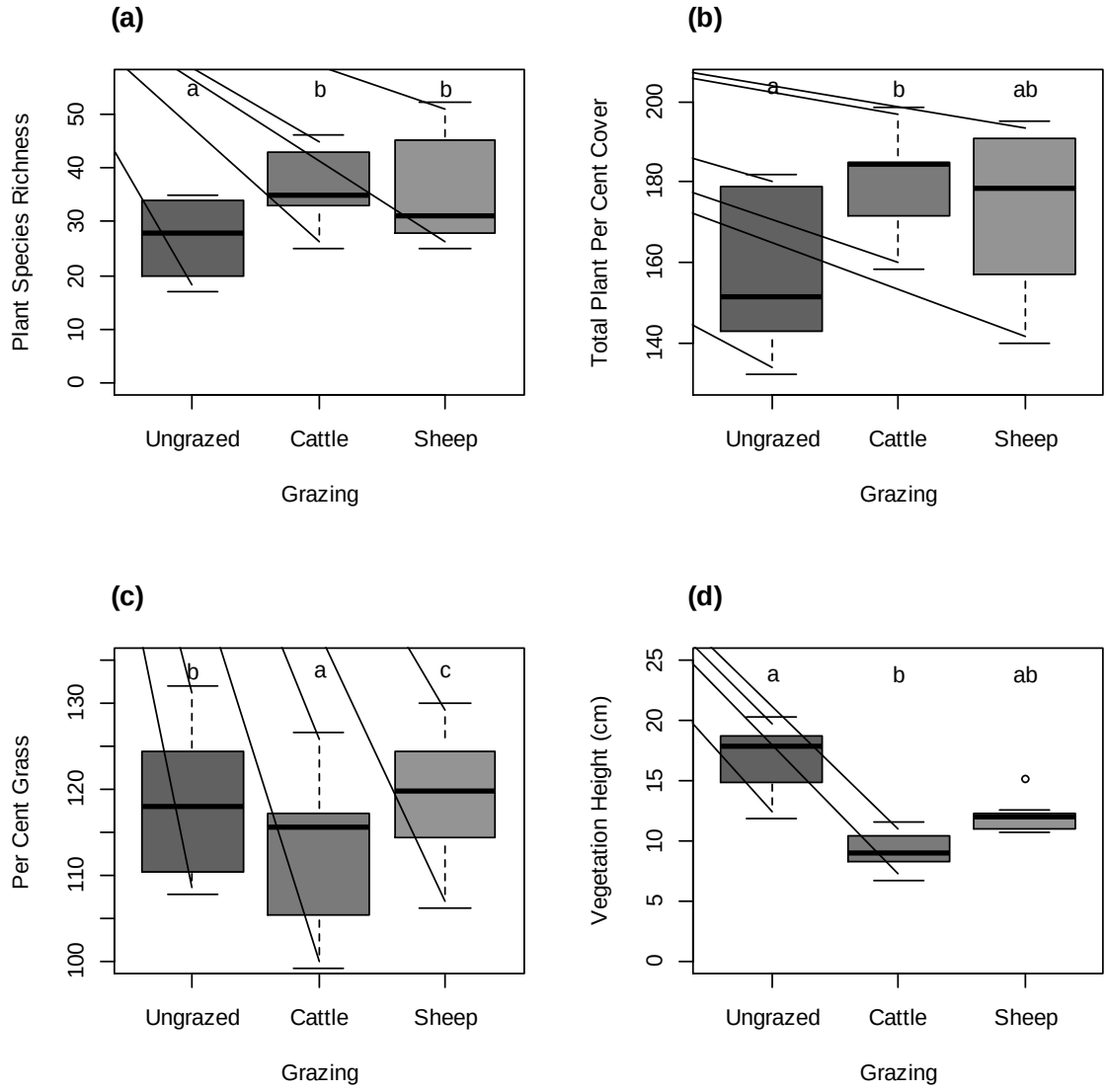

Figure 2 Boxplot of (a) plant species richness, (b) total plant per cent cover, (c) per cent cover of grass and (d) vegetation height among grazing regimes. The letters indicate significance of post hoc Tukey test, where letters are the same this indicates no significant difference.

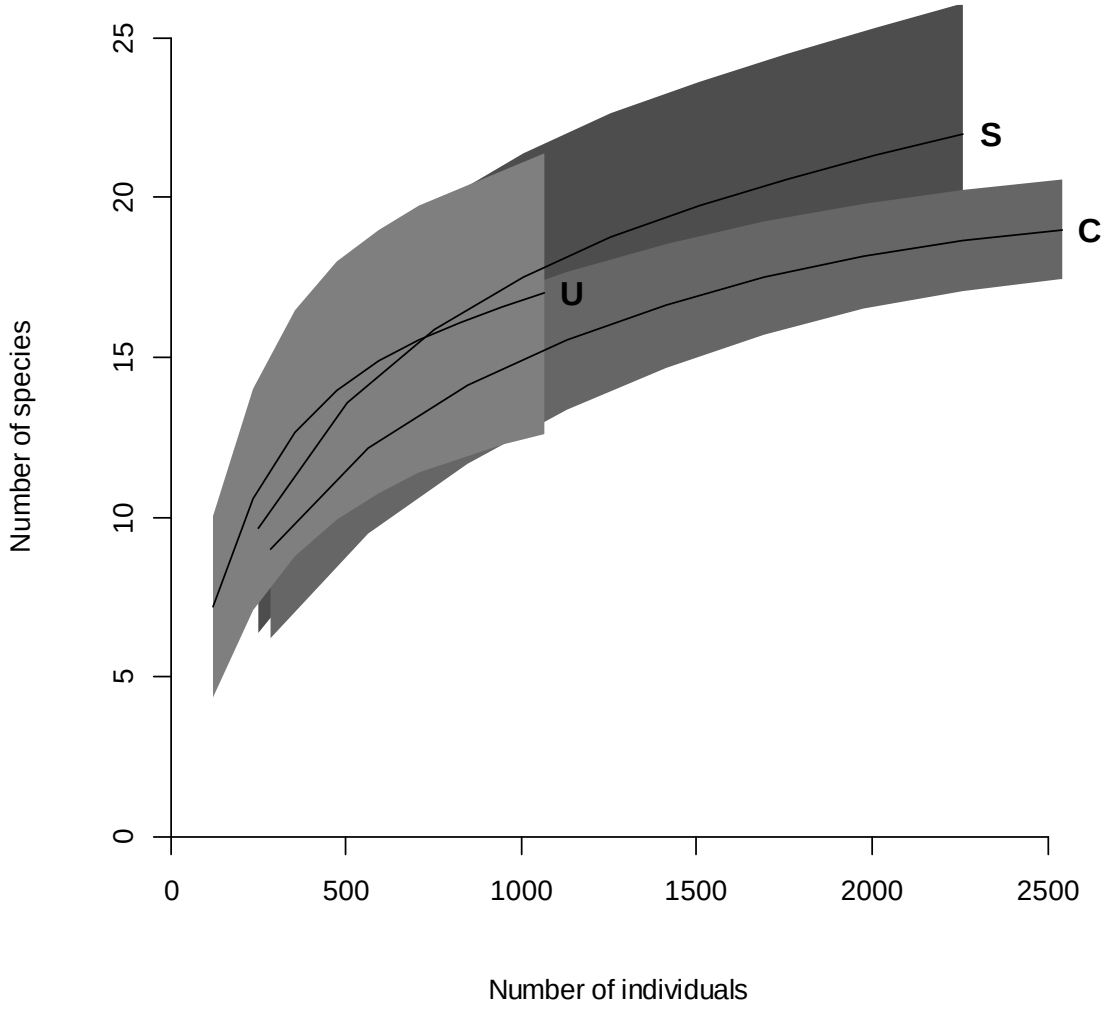

Figure 3 Sample based rarefaction curves scaled by the number of individuals, indicating carabid beetle species richness. U=ungrazed, S=sheep grazed and C=cattle grazed. Grey bars indicate 95% confidence intervals

Plant and carabid beetle species compositions among grazing regimes

Seven plant species were strongly associated with cattle grazing, one with sheep grazing and one with ungrazed regimes (Table 2). All were patch forming and of the six vascular plants the vegetative spread of three species was creeping, two species were tussock forming and one showed no vegetative spread. Of the carabid beetle species two were strongly associated with sheep grazing (*C. violaceaus* indicator value = 0.64, p = 0.004; *Synchus vivalis* indicator value = 0.65, p = 0.004) and one associated with cattle grazing (*C. arvensis* indicator value = 0.74, p = 0.0002). The declining *C. violaceaus* (Brooks *et al.* 2012) had a strong association with sheep grazing, whilst the nationally scarce *Pterostichus cristatus* (1 individual) and *Pterostichus aethiops* (5 individuals) were also present in this regime, though not identified as being significantly associated with it. In addition, the only carabid beetle species associated with cattle grazing, *C. arvensis*, is in decline in Britain (Brooks *et al.* 2012).

There were significant differences in species composition of plants amongst grazing regimes ($F_{2, 24} = 2.60$, $p < 0.001$). The covariable of region accounted for 24.8% of the variability in the overall model. The first two PCA axes accounted for 41.2% of variability in the unconstrained species data (represented in the ordination biplot; Fig. 4), and cumulatively PCA axes 1-4 accounted for 57.1% of the variability in the unconstrained species data (Table 3). Cattle grazed and sheep grazed regimes display overlap along both axes whilst ungrazed regimes are separated in ordination space from cattle grazed regimes on PCA2. Further, cattle grazed and ungrazed regimes have an even spread along PCA1 with sheep grazed regimes displaying a tighter cluster. The tighter clustering of sheep grazed regimes along PCA1 reflects greater homogeneity than both cattle grazed and ungrazed regimes.

Carabid beetle species compositions also differed significantly amongst grazing regimes ($F_{2, 24} = 2.16$, $p < 0.001$). Multivariate dispersion was also significant amongst regimes ($X^2_{(2, N = 27)} = 6.14$, $p < 0.05$) though a post hoc test revealed no differences. However, significant differences in carabid beetle species composition among grazing regimes found by PERMANOVA are supported by the PCA plot (Fig. 5) where there is overlap of sheep grazed sites and cattle grazed sites on both axes, whilst ungrazed sites are mostly separated from cattle grazed sites on PCA2. The covariable of region accounted for 36.6% of the variability in the overall model. The first two PCA axes accounted for 44.6% of variability in the unconstrained species data (represented in the ordination biplot; Fig. 5), and cumulatively PCA axes 1-4 accounted for 70% of the variability in the unconstrained species data (Table 4).

Concordance between plant and carabid beetle species compositions

There was significant concordance between species composition ordinations (Correlation in a symmetric Procrustes rotation = 0.42, p = 0.015). However, this was not sufficiently strong (>0.7) to regard vegetation as a proxy for carabid beetles (Heino, 2010; Sauberer, 2004). Examination of distance between coordinates revealed no significant difference amongst grazing regimes ($F_{2, 24} = 0.345$, $p = 0.71$) indicating that the pattern of concordance in the overall model holds true across all regimes. There was no significant correlation between plant species richness and carabid beetle species richness ($r_{s\ (N= 25)} = -0.08$, $p = 0.67$).

Table 2 Vascular plant and bryophyte species associated with grazing regime. Indicator Species Analysis produces an Indicator Value between 0 – 1, with values closest to 1 signifying a perfect indictor (always present in a particular treatment and exclusive to that treatment). P values signify significance of Indicator Values for each species based on Monte Carlo randomisation procedure with 4999 iterations. Selected vascular plant traits were gathered from Peat, Fitter and Ford (2015).

Species	Indicator Value	p	Associated Grazing	Normal method of propagation		Vegetative Pattern	Clonality
Vascular Plants							
Carex panicea	0.54	0.017	Cattle	Vegetative		Patch forming	Rhizome far creeping
Carex flacca	0.50	0.005	Cattle	Vegetative		Patch forming	Rhizome far creeping
Danthonia decumbens	0.46	0.02	Cattle	Seed		Patch forming	Tussock forming graminoid
Thymus polytrichus	0.50	0.004	Cattle	Seed and vegetative		Patch forming	Extensively creeping and rooting at nodes
Anthoxanthum odoratum	0.57	0.0122	Sheep	Seed		Patch forming	Tussock forming graminoid

Stachys officinalis	0.44	0.178	No Grazing	Seed and vegetative		Patch forming	Little or no vegetative spread
Bryophytes							
Pseudoscleropodium purum	0.51	0.015	Cattle				
Dicranum scoparium	0.68	0.0002	Cattle				
Racomitrium lanuginosum	0.56	0.0178	Cattle				

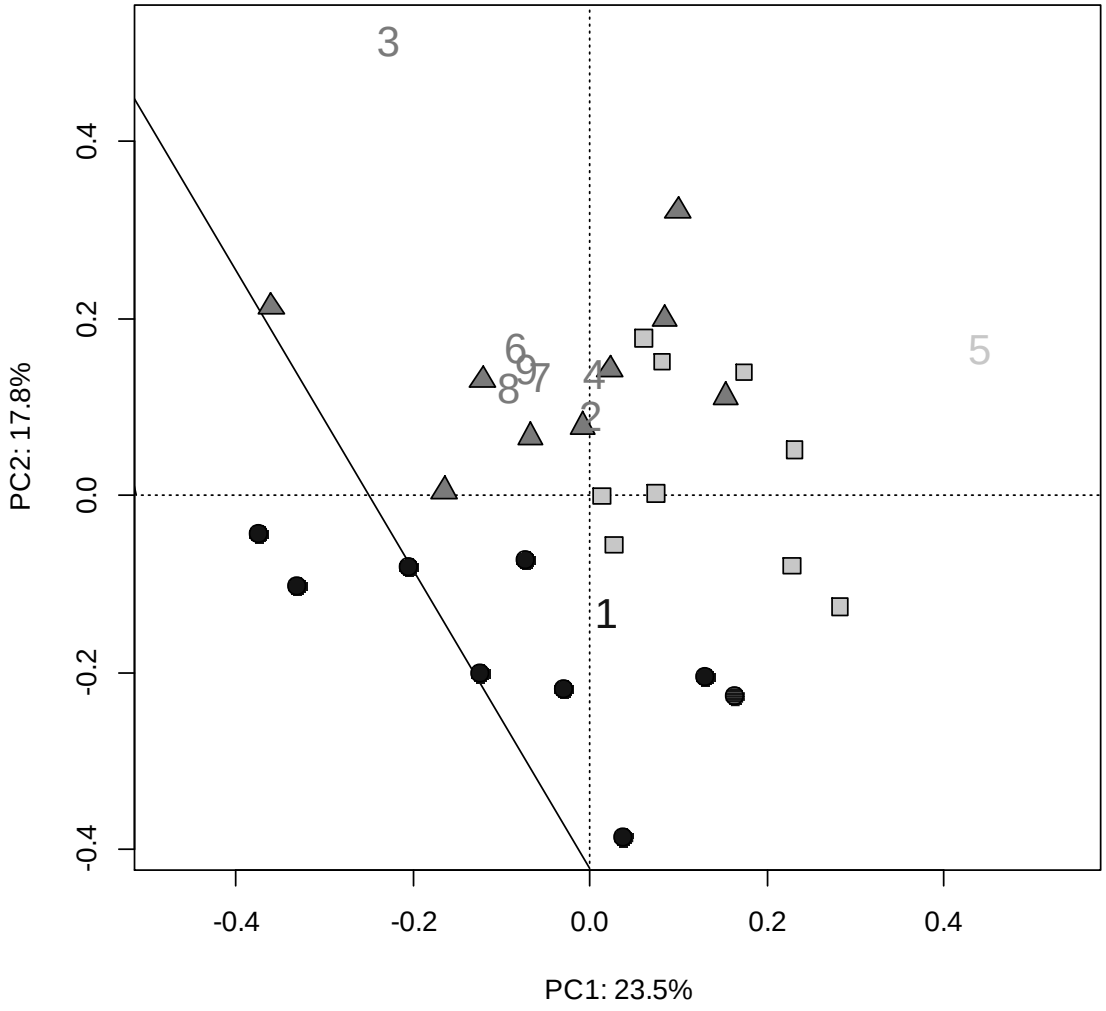

Figure 4 Principal Components Analysis of vegetation species data with the effects of location partialled out. Indicator species with significance of <0.05 are displayed as weighted species scores. Circles are ungrazed, triangles are cattle grazed and squares are sheep grazed. Numbers represent indicator species as follows: 1 – *Betonica officinalis*, 2 – *Carex panicea*, 3 – *Carex flacca*, 4 – *Danthonia decumbens*, 5 – *Anthoxanthum odoratum*, 6 – *Thymus polytrichus*, 7 – *Pseudoscleropodium purum*, 8 – *Dicranum scoparium*, 9 – *Racomitrium lanuginosum*.

Table 3 Summary of plant species PCA results. Eigenvalues and their contribution to total variance is after the removal of the conditioning variable 'region'. Total Variance* is after removal of the conditioning variable 'region'.

	Axis 1	Axis 2	Axis 3	Axis 4	Total Variance *
Eigenvalues	0.251	0.190	0.089	0.080	0.107
% Variance Explained	23.5	17.8	8.3	7.5	100

Table 4 Summary of carabid beetle species PCA results. Eigenvalues and their contribution to total variance is after the removal of the conditioning variable 'region'. Total Variance* is after removal of the conditioning variable 'region'.

	Axis 1	Axis 2	Axis 3	Axis 4	Total Variance *
Eigenvalues	0.041	0.034	0.025	0.018	0.170
% Variance Explained	24.4	20.1	14.9	10.4	100

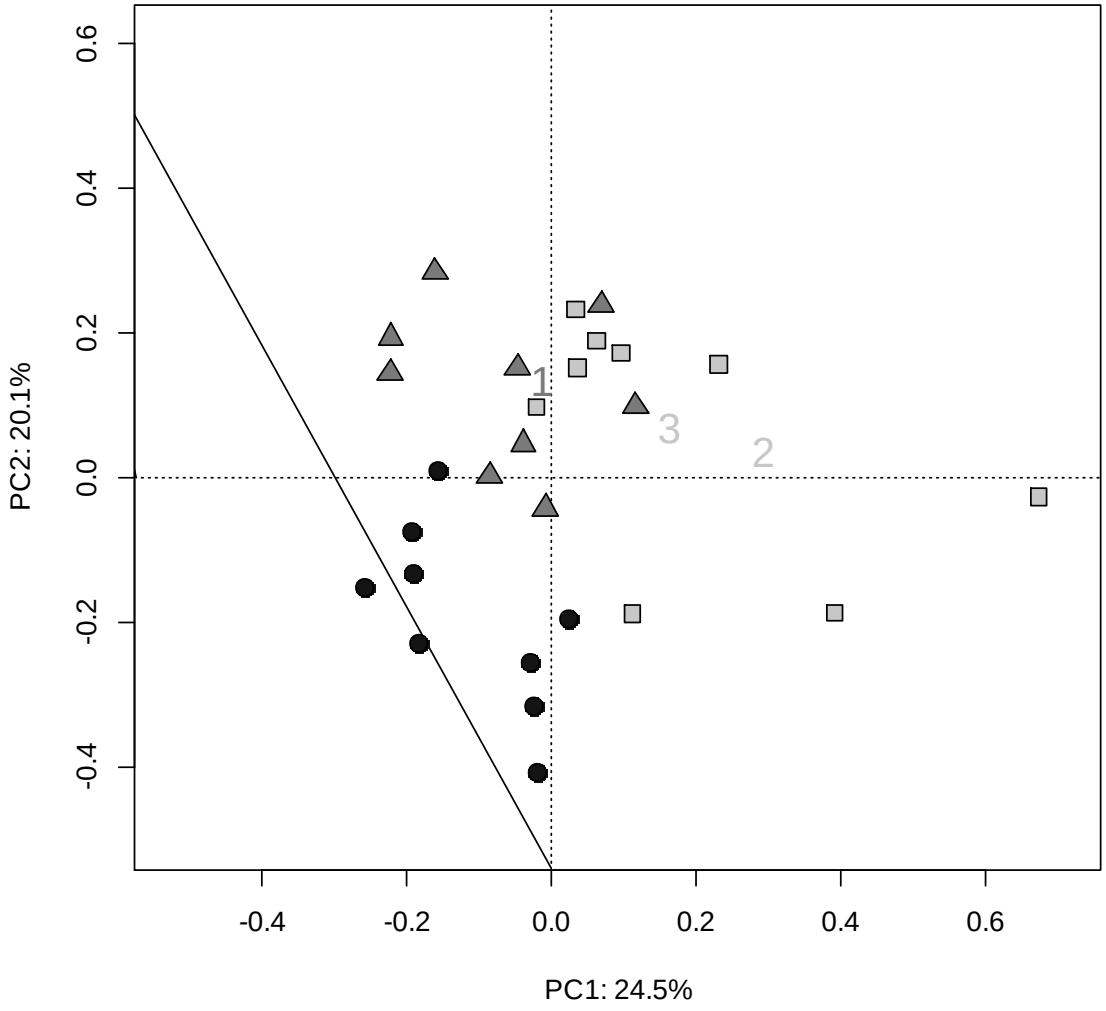

Figure 5 Principal Components Analysis of carabid beetle species data with the effects of geographical location partialled out. Indicator species with significance of <0.05 are displayed as weighted species scores. Circles are ungrazed, triangles are cattle grazed and squares are sheep grazed. Numbers represent indicator species as follows: 1 – *Carabus arvensis*, 2 – *Synchus vivlais*, 3 – *Carabus violaceus*.

Discussion

Plant and carabid beetle species diversity among grazing regimes

This study found reduced plant species richness in ungrazed locations, supporting hypothesis one that grazed locations would have greater plant species richness than ungrazed locations. This is in accord with the intermediate grazing optimisation model which suggests that plant species richness reaches a maximum at intermediate biomass as a product of optimum grazing levels (Grime, 1973; Oba *et al.* 2001). Deviation either side of this, through increased grazing or reduced grazing, results in reduction in plant species richness as observed in ungrazed regimes in the present study. This is likely to be a result of reduced light in ungrazed regimes due to increased vegetation height and encroachment of grasses (Bakker *et al.* 2003; Jacquemyn *et al.* 2003, 2011). Further, reduced plant species richness may be a result of decreased germination opportunities from a reduction in gaps in the sward (Grubb, 1977; Jacquemyn *et al.* 2003, 2011). In contrast, and in line with previous studies (Partel *et al.* 1998; Pykala, 2003), plant species richness was greater in grazed regimes, whilst vegetation height was lower.

Among grazing types plant species richness did not differ between sheep grazing and cattle grazing. However, the proportion of cover of grasses was higher under sheep grazing than cattle grazing. Grant *et al.* (1985) found that sheep diet was more varied and contained more forbs and less grass stems than that of cattle. This may explain the increased cover of grasses in sheep grazed locations in the present study and the strong association of *Anthoxanthum odoratum*, a competitive grass that is grazed less preferentially by sheep when other more palatable grasses are available (Lopez *et al.* 2003) such as *Sesleria caerulea* and *Agrostis capillaris* in this case.

The results did not support hypothesis two that carabid beetle species richness would be greater in grazed compared to ungrazed regimes as a product of greater habitat heterogeneity. Instead, carabid beetle species richness did not differ among grazing regimes, despite differences in plant species richness and vegetation height between grazed and ungrazed regimes. There were, however, differences in carabid beetle abundance between grazed and ungrazed regimes, which may reflect greater breadth of resources. In contrast, similarity in species richness may be reflective of little niche differentiation among grazing regimes. Kaltas *et al.* (2013) found that carabid species richness was greater at intermediate rather than low intensity grazing. Indeed, increased carabid beetle richness may require greater disturbance than the low intensity grazing regimes in the present study.

Plant and carabid beetle species compositions among grazing regimes

There was a distinct difference in species composition for both taxon groups, supporting hypothesis three. Species composition of plants differed among grazing regimes (Fig. 4) as hypothesised, matching results of previous studies (Kohyani *et al.* 2008; Veen *et al.* 2010). The removal of plant biomass through grazing alters competitive relationships amongst plants which drives both heterogeneity and preserves diversity (Bullock and Marriott, 2000; Rook *et al.* 2004; Scimone *et al.* 2007). It is likely that differences in plant species composition among grazing regimes in the present study are a product of this altered competitive relationship. Indeed, plant species that were strongly associated with cattle grazing are all patch forming and of these, all but one of the vascular indicator species favoured method of propagation is vegetative. This enables them to colonise bare gaps left

when cattle indiscriminately remove tufts of vegetation, even when seed germination is not possible as in Bullock *et al.* (2001).

In ungrazed regimes, the species composition of carabid beetles was distinct from those in grazed regimes, akin to the vegetation results. Differences in carabid beetle species composition among grazing regimes in the present study may be a product of different plant species compositions and vegetation height. Indeed, such small-scale vegetation differences influence available resources for carabid beetles including prey and other food, microclimate etc. (Thiele, 1977).

Species that had strong associations with grazing included those from the genus *Carabus*. Under both grazing regimes tussock forming grasses were identified as associated species (*A. odoratum* and *Danthonia decumbens*) which may act as places of refuge for both *Carabus* species found to be associated with grazing here. Dennis *et al.* (1997) found that *C. violaceaus* was associated with short term ungrazed *Nardus stricta* grassland which had an average sward height of 8 – 12cm. However, the present study found an association of *C. violaceaus* with extensively grazed sheep calcareous grassland rather than those which had been ungrazed long term, whilst *C. arvensis* was associated with cattle grazing. Grazing produces more spatially heterogeneous vegetation (Grandchamp *et al.* 2005; van Wieren, 1995) and associations of *Carabus* species with grazing in this study may be due to greater plant spatial heterogeneity. The removal of selected plant species during sheep grazing, or larger tufts under cattle grazing, often results in patches of shorter vegetation containing taller tufts, which are preferred conditions for many *Carabus* species (Butterfield *et al.* 1995; Cole *et al.* 2010). This may account for the greater abundance of

Carabus species in grazed regimes (146 individuals) than in ungrazed regimes (11 individuals).

Conservation significance and management recommendations

The present study demonstrates the differing impacts of three commonly used grazing regimes in upland calcareous grassland, sheep grazing, cattle grazing and no grazing on vegetation and carabid beetles and indicates that both taxonomic groups respond differently to grazing and no grazing. Under no grazing and sheep grazing the plant species composition becomes more homogeneous, with dominance of grass. While there are no associations between any rare plant species and any particular grazing regime there are important implications for carabid beetle diversity.

Interestingly, despite the absence of forest cover in the upland landscapes studied, several carabid beetle species recorded in the present study are usually associated with forest habitats in mainland Europe e.g. *Abax parallelpipedus, P. aethiops, Harpalus latus, Stomis pumicatus*. Forests occupy 13% of the total UK land area (Forestry Commission, 2013) though this figure was as low as 5% in 1900 (Atkinson and Townsend, 2011). It has been suggested that forest carabid species have adapted to occupy dwarf shrub communities in Britain (Anderson *et al.* 2000). It may also be the case that such species have adapted to inhabit grasslands due to appropriate microclimatic conditions. Within the present study the calcareous grassland occurs within a matrix of upland heath and limestone pavement, the former of which has a relict woodland floor plant community, carabid communities may be influenced by these neighbouring habitats and their management should also be considered.

Species composition of plants influences structural characteristics within grasslands (Woodcock *et al.* 2007) which in turn influences invertebrate composition by providing refuge, food resources and suitable hunting grounds (Dennis *et al.* 2001; Morris, 2000; Vickery *et al.* 2001). Woodcock *et al.* (2005) found a positive correlation between plant diversity and grass cover with beetle diversity. Results from the present study identify a statistical correlation between species composition of plants and carabid beetles. However, this could not be considered to be ecologically valid as the correlation coefficient was less than 0.7, the level above which one taxonomic group may be considered as an indicator of another (Heino, 2010; Sauberer *et al.* 2004). In addition, there was no relationship between plant species richness and carabid beetle species richness, concurrent with previous studies (Finch and Löffer, 2010; Jonsson and Jonsell, 1998; Sauberer *et al.* 2004). Results for both community composition and species richness suggest that neither are appropriate indicators of carabid beetle diversity

Populations of both *C. violaceus* and *C. arvensis* have declined by 10-20% and 60-70% respectively in the past decade (Brooks *et al.* 2012). The association of *C. violaceaus* and the presence of the nationally scarce *P. cristatus* and *P. aethiops* with sheep grazing warrants the recommendation of continuation of this management regime. The importance of cattle grazing is also highlighted by the heterogeneous nature of the plant species composition and the association of the declining *C. arvensis*. The unique nature of the carabid beetle species composition in ungrazed regimes, including the presence of the nationally scarce *P. aethiops*, is also noted. Hence, it is recommended that conservation organisations consider a landscape scale approach to these high nature value grasslands that incorporates low intensity cattle grazing, low intensity sheep grazing and ungrazed areas as an alternative to high intensity sheep grazing.

Plant species composition and richness did not indicate change in that of carabid beetles. Further, carabid beetles did not always respond in the same way as plants to grazing regime, suggesting that conservation managers should exercise caution when using plant species composition or broad measures of plant diversity to indicate biodiversity value, identify priority habitats or select grazing regimes to support a particular habitat condition.

Chapter 3

Spider assemblage responses to vegetation structure under contrasting grazing management in upland calcareous grasslands

Prepared for submission to *Journal of Insect Conservation and Diversity*

Abstract

1. Calcareous grassland is one of the most species rich and diverse habitats within Europe, but has faced decline due to agricultural intensification and abandonment. In recent years conservation organisations have altered grazing practices in an attempt to maintain floristic components. However, there has been little consideration of the effects of the changes in grazing practice on invertebrate communities. This study determines the impacts of commonly used grazing practices in upland calcareous grasslands on spiders in relation to vegetation structural complexity.

2. Typical grazing management regimes (light cattle, light sheep, heavy sheep and ungrazed) were examined in three regions of upland calcareous grassland in Britain. Spiders were sampled using pitfall traps from April – August 2014 and vegetation structural complexity was recorded in 2m x 2m quadrats paired with pitfall traps sequentially throughout the sample period.

3. There were three distinct spider assemblages among the grazing regimes; ungrazed, heavy sheep grazed and a third assemblage shared between light cattle and light sheep grazing. The distinct spider assemblages among grazing regimes can be attributed to the interaction of grazing and habitat structure. Though abundance differed among grazing regimes spider species richness did not.

4. Increased vegetation structural complexity in ungrazed regimes resulted in an assemblage dominated by the guild ‘sheet web weavers’ (dominated by the

Linyphiidae family). In contrast, reduced vegetation structural complexity and homogeneity in heavy sheep grazing resulted in an assemblage dominated by the 'other hunters' guild (including *Oedothorax* and *Erigone* genera).

5. Grazing regime alters vegetation structural complexity and is important in supporting distinct spider assemblages. This research indicates that low intensity conservation grazing regimes, in addition to no grazing, should be promoted across upland calcareous grassland landscapes to maintain heterogeneity.

Introduction

Calcareous grassland is among the most species rich and diverse habitats in Europe, supporting a range of specialised flora and fauna (Wallis de Vries *et al.* 2002; Poschlod & Wallis de Vries, 2002). Due to wide scale loss and degradation following mid-20th century agricultural intensification, it is currently the focus of conservation efforts and is protected in international legislation (e.g. EU Habitats Directive) (Willems, 2001; Fischer and Stocklin, 1997; Poschlod *et al.* 2005; Roesch *et al.* 2013; Wallis de Vries *et al.* 2002). However, despite the great diversity of both flora and fauna, conservation management, which is typically performed through grazing with livestock, generally aims to maintain particular plant communities through prevention of succession and domination by one or few species (Willems, 2001; Wallis de Vries *et al.* 2002). Further, monitoring of conservation management treatments mostly refers only to vegetation (Poschlod & Wallisde Vries, 2002). This single taxon approach to conservation management and monitoring fails to recognise the importance of invertebrates, or the impact that contrasting management has on them, in these internationally important habitats.

Selection of grazing regime has implications for invertebrate communities through its effects on plant community composition and vegetation structural complexity (Chapter 2, this thesis; Dennis *et al.* 2015; Dennis *et al.* 2001; Morris, 2000; Vickery *et al.* 2001; Krauss *et al.* 2003; Woodcock *et al.* 2005)). For example, the decline in vegetation structural complexity associated with high stocking densities results in the loss of spiders which are dependent upon aerial structures and plant litter e.g. large web weavers (Deng *et al.* 2014; Dennis *et al.* 2001; Gibson *et al.* 1992). In contrast, some spiders require the less structurally complex, more open swards created by higher intensity grazing e.g. *Erigone*

spp (Bell *et al.* 2001; Gibson *et al.* 1992). Further, spider abundance and species richness increases with reduced stocking density due to greater vegetation structural complexity and reduced disturbance (Dennis *et al.* 2015; Woodcock *et al.* 2009; Horváth *et al.* 2009).

Spiders are among the most abundant animals in terrestrial ecosystems and occupy an important role in terrestrial food webs as both predators and prey (Turnbull, 1973; Uetz, 1991). They are sensitive to changes in plant structural complexity which renders them useful indicators of habitat change (Dennis *et al.* 2001, 2015; Prieto-Benitez and Méndez, 2011; Duffey, 1962; Uetz, 1991; Marc et al, 1999). Their habitat requirements in grasslands differ among species with some such as *Ceratinella brevipes* (Westring, 1851) and *Allomengea scopigera* (Grube, 1859) favoured by more structurally complex vegetation with deep litter layers (McFerren *et al.* 1994; De Keer *et al.* 1989). Whilst less structurally complex vegetation favours pioneer species characteristic of disturbed land such as those from *Erigone* and *Oedothorax* genera (Noel and Finch, 2010; Downie *et al.* 2000; McFerren *et al.* 1994; Malfait and De Keer, 1990). Differences in spider species associations with vegetation structure are also linked to spider hunting strategies (Uetz, 1991; Alderweireldt, 1994; Bell, *et al.* 2001). Ground hunting species such as those from the *Pardosa* genus require a heterogeneous sward of open patches to search for prey and taller vegetation for refuge (Malfait and De Keer, 1990), whereas orb web weaving spiders select structurally complex vegetation that provides increased web anchorage points (Diehl *et al.* 2013; Langellotto and Denno, 2004; McNett and Rypstra, 2000). Differences in foraging strategy, activity and substrate utilisation amongst species make grouping spiders into guilds an appropriate way to examine environmental impacts on them (Corcuera *et al.* 2015; Schweiger *et al.* 2005).

Not unlike calcareous grasslands elsewhere in Europe, upland calcareous areas within Britain experienced decline due to intensive grazing, typically with sheep (Dennis *et al.* 2008; Fuller and Gough, 1999). Over the last 15 years, in an attempt to conserve the characteristic vegetation of this habitat, changes in management have occurred based on the perceived benefit to the plant community. This has typically involved a shift from grazing with high numbers of sheep to lower stocking densities of cattle, though occasionally some areas are managed with lower stocking densities of sheep or no grazing. Research has shown a decline in invertebrate species richness in response to increased grazing intensity in a lowland limestone grassland (Gibson *et al.* 1992), and research in other upland grasslands types has shown an increase in invertebrate abundance in response to reduced grazing intensity (Dennis at al. 2001). However, there has been no research which tests the impacts of low intensity conservation grazing regimes on invertebrates in these internationally important upland calcareous grasslands.

This study aims to address this knowledge gap, being the first to determine the impact of high intensity sheep, low intensity sheep, low intensity cattle and ungrazed regimes on spider assemblages in upland calcareous grasslands of conservation importance. Further, this study explores how structural complexity, and its interaction with grazing, drives differences in spider assemblages. These findings are discussed in the context of upland calcareous grassland conservation and the role that grazing prescription can play in maintaining and enhancing a diverse spider fauna.

Methods

Study Sites

Four grazing regimes - ungrazed, light intensity cattle grazed, light intensity sheep grazed and high intensity sheep grazed (hereafter referred to as light sheep and heavy sheep respectively) - were selected for study within the most extensive upland limestone areas in the UK.

Each grazing regime was replicated across three geographically distinct regions separated by 17-47km in Northern England (54°29′18.55″N, 002°32′33.00″W) (54°11′43.30″N, 002°21′00.13″W) (54°08′50.69″N, 002°06′32.54″W). In each region four extensive areas of limestone grassland (size 12 ha – 526 ha, median 42.5 ha) were selected within which three sampling locations were established. These were separated by a minimum of 72m (median 269m) to ensure statistical independence of samples (Digweed *et al.* 1995), and a minimum of 50m from the edge of the grazing regime and away from disturbance e.g. footpaths, water troughs etc. Spatial independence of samples was confirmed with Moran's I test based on nearest neighbour distances for all 36 locations for spider abundance, showing there was no significant spatial autocorrelation (Moran's I ± SD: -- 0.07 ± 2.60, p = 0.99) (Bivand *et al.* 2014).

Across all sampling locations the current grazing regime had been in place for at least ten years prior to investigation. Cattle and light sheep grazed regimes were lightly grazed for the conservation of upland calcareous grassland with stocking densities of less than 0.24 Livestock Units per Hectare per Year (LU ha^{-1} y^{-1}), whereas heavy sheep grazed regimes

had a stocking ratio of more than 0.36 LU ha^{-1} y^{-1} (Backshall *et al.* 2001) calculated as:
Annual Equivalent Stocking Density = ((N*GLU/H)*(M/12)

Where: N = Number of individuals, GLU = Grazing Livestock Unit (taken from Nix, 2004), H = Hectares and M = Number of months grazed.

Elevation ranged from 288 – 396m, median 335m. Soil across the sites was generally base rich with some deposits of glacial till and peat. All areas were characterised by a mix of calcareous grassland, upland heath and limestone pavement, and were surrounded by a mix of extensively and intensively grazed open grassland. Typical areas of calcareous grassland were selected for study using detailed habitat maps and aerial photographs. Within each location, surveys of vegetation and epigeic spiders were conducted between May – August 2014.

Spider Sampling

Within each sampling location a line of six pitfall traps, spaced 2m apart, were established to capture spiders. Traps consisted of a plastic cup approximately 7cm in diameter and 9cm deep and were covered with a square plastic lid suspended 1cm from the ground by pegs to prevent rain water and debris from entering. These were filled with 1cm depth of antifreeze to act as a killing and preserving agent. To prevent traps being trampled or interfered with by livestock, in grazed areas each trap was protected by a secured cage made from 2.5cm x 2.5cm gauge mesh. These cages do not affect the trapping rates of ground-dwelling invertebrates (Oxbrough *et al.* 2012). Traps were set between 01/05/2014 and 22/08/2014 and were changed every 21 days, giving a total of 105 trap days. Samples from five of the traps within each location were pooled for analysis.

All adult spiders were identified to species level using Roberts (1993) and nomenclature follows the World Spider Catalogue (2017). Information on conservation status was gathered from Dawson *et al.* (2008). Since it was not possible to reliably identify most juvenile species these were excluded from the study. Spider reference specimens are housed at the Edge Hill University Department of Biology arthropod collection.

Spider Hunting Guilds

Following identification of spiders to species, they were divided into six separate guilds based on hunting strategy as suggested by Cardoso *et al.* (2011): sheet web weavers, ground hunters, space web weavers, orb web weavers other hunters and ambush hunters. The list of spider species and associated guilds is included in Appendix A2.

Vegetation Structural Complexity Measurements

Within 1m from pitfall traps, two 2m x 2m quadrats, spaced 2m from each other were set up at approximately three week intervals from 6th May 2014 to 1st August 2014, giving a total of 10 quadrats per sampling location. Within each quadrat the vertical distribution of vegetation was recorded as the number of 'contacts' in each 5cm height interval of a pin 5mm in diameter passed vertically through the vegetation at 10 points (separated by 15cm), a method adapted from Wiens (1974), Woodcock *et al.* (2007) and Azpiroz and Blake (2016). The type of vegetation in contact with the pin was also recorded as graminoids, thatch (dead vegetation), moss and herbs. Data from all 10 pins per quadrat were summed to give a single unit of structural complexity per quadrat. The median of this unit of structural complexity was then calculated for all ten quadrats at each sampling location to account for seasonal variation, giving a single unit of structural complexity per sampling

location for the entire sampling period. Within each quadrat per cent cover of all vascular plants and bryophytes was estimated to the nearest five per cent. Per cent cover data collected at each sampling location for the duration of the sampling period was averaged, giving a single measurement of vegetation cover from the 10 quadrats recorded at each location.

Data Analysis

To account for differences in trapping effort due to trap loss all samples were standardised by trap day by calculating the abundance of each species at each location and dividing it by the number of actual trap days at that location and then multiplying it by the maximum number of trap days across all locations (105) a standard method in studies using pitfall trapping (Bergeron *et al.* 2013; Blanchet *et al.* 2013: Pinzon *et al.* 2013).

All statistical analyses were carried out with R statistical software version 3.3.2. (R Core team, 2016) with the exception of rarefaction curves calculated using EstimateS version 9.1.0 (Colwell, 2013).

Differences in spider species richness were examined with raw species data (not standardised by trap day) using sample based rarefaction scaled by the number of individuals. This technique accounts for differences in sampling effort by standardising species richness for the number of individuals within a sample. Rarefaction estimates the number of species expected in a random sub-sample extracted from a larger sample (Magurran, 1988, 2004).

Differences in spider abundance (as measured by the accumulated catches at each location) among grazing regimes were examined with Generalised Linear Mixed Models (GLMMs)

performed with Poisson errors using the glmer function of the lme4 package (Bates *et al.* 2015). The interaction of grazing regime and vegetation structural complexity was modelled as a fixed factor with region modelled as a random factor. The model was tested for over dispersion of Poisson errors and was found to be overdispersed (dispersion = 24.12). To combat overdispersion the model was recalculated using negative binomial errors (Thomas, 2017). The model was tested for significance using the Anova function of the Car package (Fox and Weisberg, 2011) and post hoc Tukey pairwise comparisons were used to test for differences among grazing regimes, correcting p values for multiple comparisons with the Holm method using the glht function of the multcomp package (Hothorn *et al.* 2008).

The impacts of grazing and vegetation structural complexity on the comparative proportion of each hunting guild were examined with GLMMs, this time computed with Binomial errors to account for the use of proportion data (Crawley, 2012). The interaction of grazing regime and vegetation structural complexity was modelled as a fixed factor with region modelled as a random factor. GLMMs were computed for sheet web weavers, ground hunters and orb web weavers. Ambush hunters, space web weavers and other hunters were not included as the data sets for each of these were too small or contained too many zero observations and instead main trends were discussed in the text. To correct for overdispersion, observation level random effects were included in the overall model (Harrison, 2014) (dispersion: sheet web weavers = 10.03; ground hunters = 26.97; orb web weavers = 30.52) and the significance of models were tested as above. Bonferonni correction was applied to the confidence intervals to account for the multiple testing of the abundance data (e.g. split into six guilds). However, as the number of species was not divided equally among the six guilds the confidence intervals at which statistical

significance was determined using the Bonferonni correction were not set equally (e.g. 0.05/6) but rather as the proportion that each guild comprised of the data set (required confidence intervals to infer significance: sheet web weavers < 0.025; ground hunters < 0.014; orb web weavers < 0.005) following Neuwald and Green (1994).

To determine if vegetation structural complexity or plant species richness was different among grazing regimes GLMMs were again performed with grazing modelled as a fixed factor and region modelled as a random factor, this time using Poisson errors in the final model as overdispersion was not detected (vegetation structural complexity dispersion = 1.19; plant species richness dispersion = 1.69). Variability of vegetation structural complexity was assessed using the Brown-Forsythe test for equality of variances, as a measure to determine structural heterogeneity within each grazing regime. Significance was tested using Kruskal-Wallis applied to the function using the lawstat package. Brown-Forsythe's test for equality of variances determines absolute deviation of scores from group medians and can be used on non-normally distributed data (Brown and Forsythe, 1974; Sheskin, 2011). To compare the proportion of vegetation structural complexity that was accounted for by thatch among grazing regimes a GLMM was performed with Binomial errors with grazing regime modelled as a fixed factor and site modelled as a random factor. The model was tested for over dispersion of Binomial errors and was found to be overdispersed (dispersion = 10.15). To correct for overdispersion observation level random effects were included in the overall model (Harrison, 2014). Proportional Bonferonni correction as above was applied, requiring a confidence interval of < 0.026 to infer significance. Thatch was examined in isolation as it constituted a large portion of the vegetation structural complexity in some regimes and is known to be important in providing refuge for some spider species (Rypstra *et al.* 1999).

Spider species composition was examined through Redundancy Analysis (RDA) computed on Hellinger transformed spider species data using the RDA function in the vegan package (Oksanen *et al.* 2016). Grazing, vegetation structural complexity and the interaction of grazing and vegetation structural complexity were included as the main terms in the model with region included as a random factor. A permutation test, with 9999 permutations, was used to test final significance of the model.

Indicator Species Analysis (Dufrene and Legendre, 1997) was computed to identify species that were strongly associated (both common and frequent) with each grazing regime using the indval function of the labdsv package (Roberts, 2015). Significance of indicator values was assessed using a Monte Carlo randomisation procedure with 4999 iterations.

Results

A total of 16 056 individual spiders were collected, of which 4162 (25.91% of overall abundance) were juveniles and 157 (0.98% of total abundance) were damaged specimens. Neither of these groups could be identified and were therefore omitted from the data set. A total of 11 737 individuals from 101 species were included in the analyses. A full list of species is given in the Supporting information S1. Overall, six species individually comprised more than 5% of the total spider abundance, together totalling nearly 60% of the total catch: *Pardosa pullata* (Clerk, 1757) (20.5%), *Pachygnatha degeeri* Sundevall, 1830 (10.25%), *Silometopus elegans* (O. P.-Cambridge, 1873) (9.5%), *Pocadicnemis pumila* (Blackwall, 1841) (7.13%), *Palliduphantes ericaeus* (Blackwall, 1853) (7.04%) and *Tiso vagans* (Blackwall, 1834) (5.5%).

Assessment of conservation status according to Dawson *et al.* (2008) revealed two endangered species: *Jacksonella falconeri* (Jackson, 1908) (50 individuals) and *Porrhomma egeria* Simon, 1884 (1 individual), and eight vulnerable species; *Agyneta subtilis* (O.P. Cambridge, 1863) (265 individuals); *Walckenareia dysderoides* (Wider, 1834) (13 individuals); *Walckenaeria inscisa* (O.P. Cambridge, 1871) (10 individuals); *Allomengea scopigera* (Grube, 1859) (7 individuals); *Trichopternoides thorelli* (Westring, 1861) (4 individuals); *Maro minutus* O.P. Cambridge, 1906 (1 individual); *Walckenaeria monoceros* (Wider, 1834) (1 individual); *Walckenaeria obtusa* Blackwall, 1834 (2 individuals).

Vegetation structure and diversity among grazing regimes

Vegetation structural complexity was significantly different among grazing regimes ($X^2_{(3, N = 36)} = 203.15$, $p<0.001$) and was driven by greater structural complexity in ungrazed compared to cattle, light sheep and heavy sheep regimes and significantly lower structural complexity of heavy sheep compared to cattle, light sheep and ungrazed (Fig. 1a). Vegetation structural complexity was significantly variable in cattle, light sheep and ungrazed regimes ($H_{N = 36} = 165.55$, $P < 0.001$; $H_{N = 36} = 221.28$, $p < 0.001$; $H_{N = 36} = 27.16$, $P < 0.001$) but not so in heavy sheep ($H_{N = 36} = 10.83$, $p > 0.21$), indicating vegetation structural complexity was homogeneous in the latter and heterogeneous in the former.

The proportion of vegetation structural complexity comprised of thatch was also significantly different among grazing regimes ($X^2_{(3, N = 36)} = 112.18$, $p<0.001$) with a greater proportion of thatch in ungrazed compared to all other grazing regimes and a significantly lower proportion of thatch in heavy sheep grazing compared to all other regimes (Fig. 1b). Plant species richness was significantly different among grazing regimes ($X^2_{(3, N = 36)} = 22.49$, $p<0.001$) and was driven by greater species richness in cattle compared to light sheep and ungrazed regimes and greater richness in heavy sheep compared to ungrazed regimes (Fig. 1c).

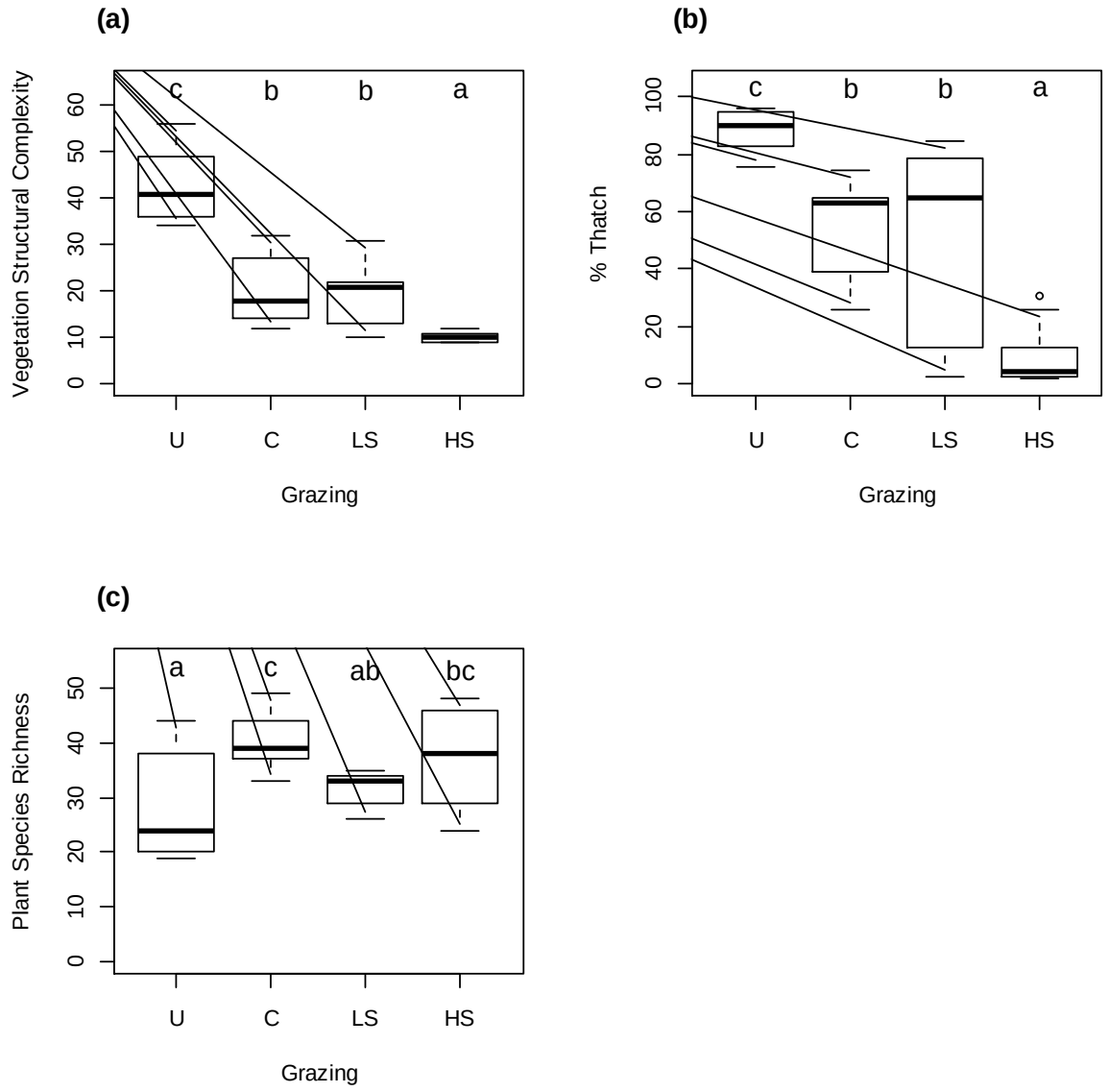

Figure 1 (a) vegetation structural complexity among grazing regimes, (b) thatch cover among grazing regimes, (c) plant species richness among grazing regimes. U= ungrazed, C = cattle, LS = light sheep, HS = heavy sheep.

Spider species diversity among grazing regimes

Rarefaction curves showed that spider species richness did not differ among grazing regimes (Fig. 2), as indicated by almost complete overlap of confidence intervals. Total spider abundance was significantly different among grazing regimes ($X^2_{(3, N = 36)} = 17.41$, $p<0.01$) though post hoc testing could not determine which grazing regimes were driving this difference, likely due to the conservative nature of these tests (and correction for multiple comparisons). However, examination of data suggests overall model significance may reflect the greater abundance in cattle and light sheep regimes compared to those of heavy sheep and ungrazed regimes (Fig. 3). There was no significant relationship between spider abundance and vegetation structure ($X^2_{(1, N = 36)} = 0.05$ $p > 0.05$) or with interaction between grazing and vegetation structure ($X^2_{(3, N = 36)} = 6.01$, $p > 0.05$).

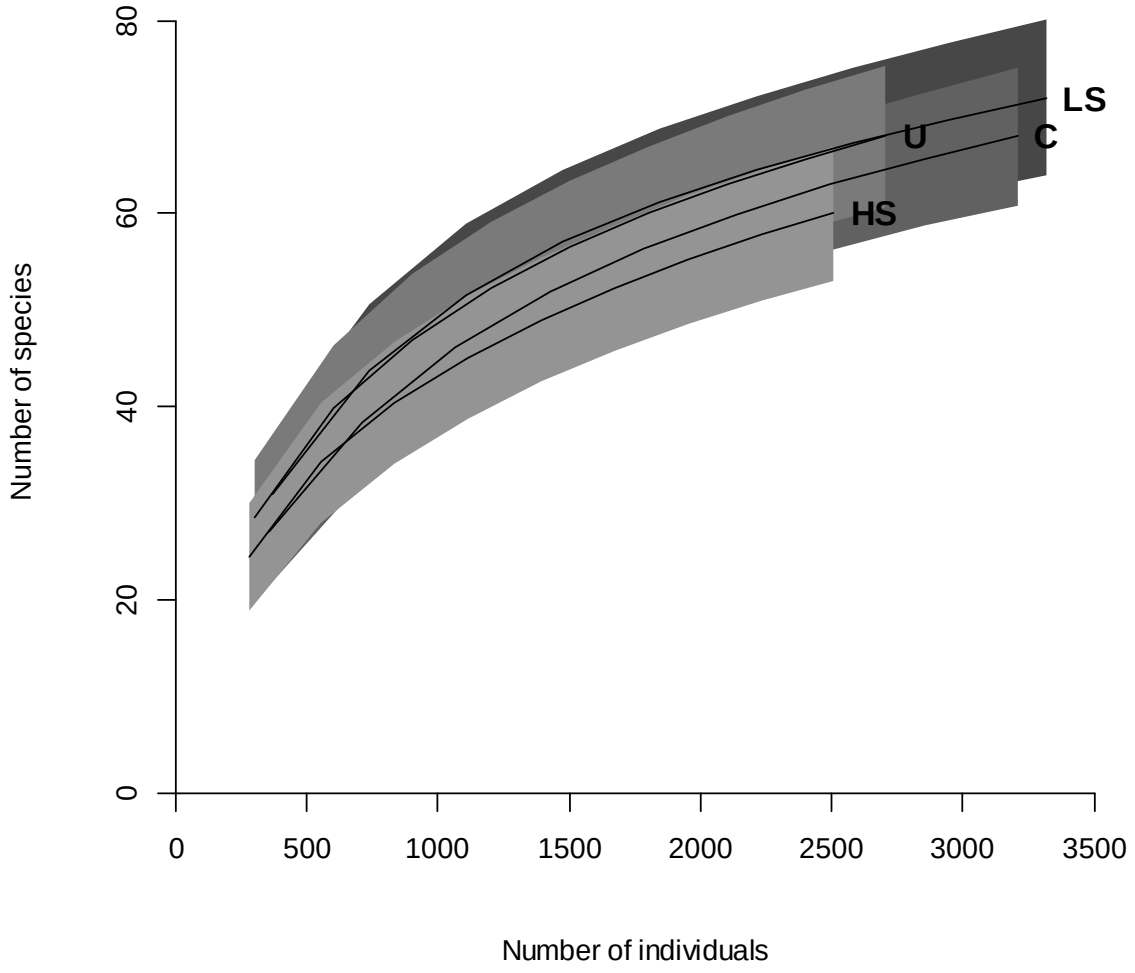

Figure 2 Sample based rarefaction curves scaled by the number of individuals, indicating spider species richness. U=ungrazed, LS=light sheep grazed, HS=Heavy sheep grazed and C=cattle grazed. Bars indicate 95% confidence intervals.

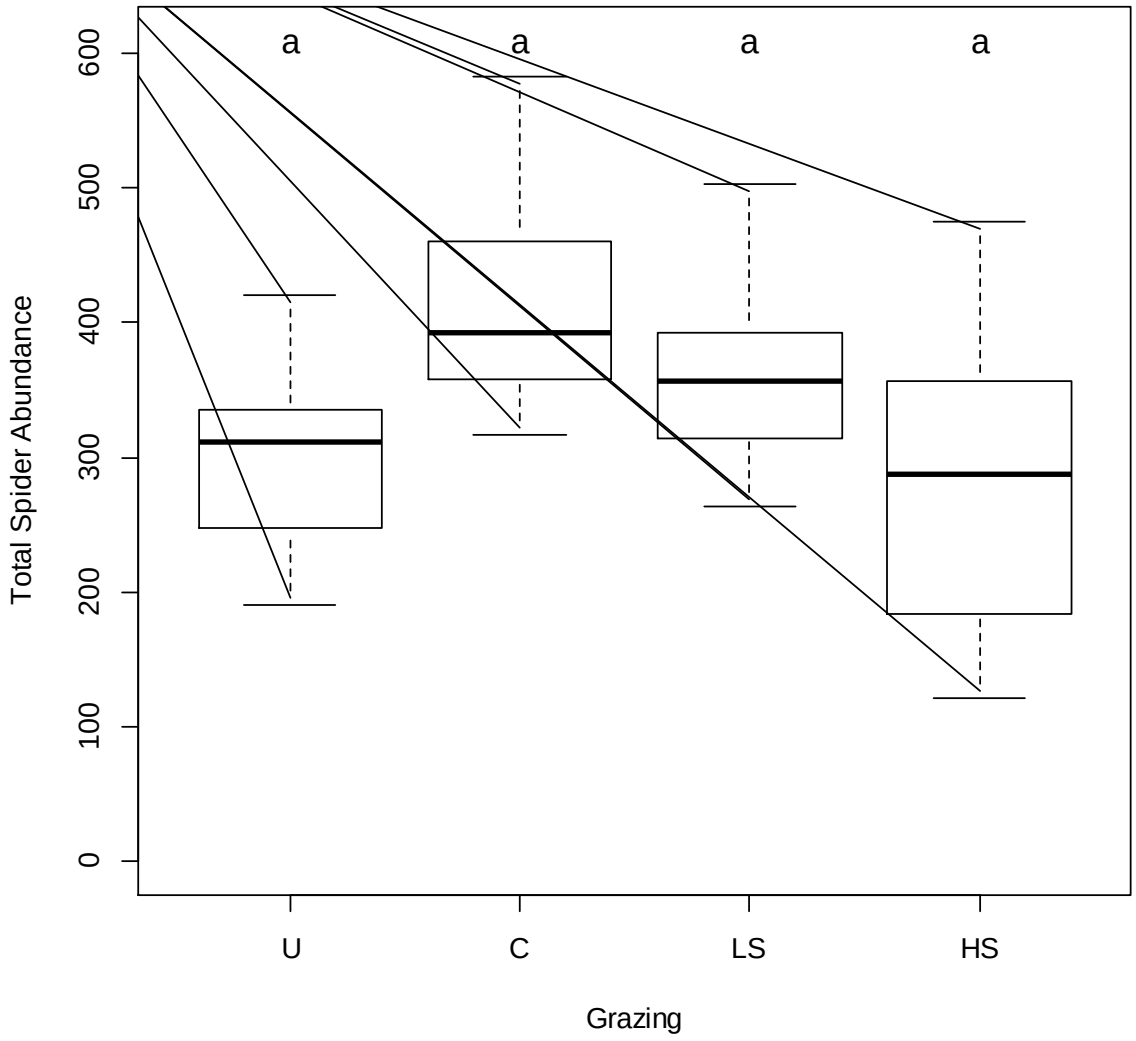

Figure 3 Spider abundance among grazing regimes. The letters indicate significance of post hoc Tukey test, where letters are different this indicates significant difference at $p < 0.05$. U= ungrazed, C = cattle, LS = light sheep, HS = heavy sheep.

Spider Guilds

The most abundant guild was the sheet web weavers (6129 individuals, 49.39%) which were mostly from the Linyphiidae family, then ground hunters (3573 individuals, 28.79%) comprised largely of Lycosidae but also Gnaphosidae and Liocranidae, orb web weavers (1291 individuals, 10.40%) which were exclusively *Pachygnatha degeeri* (Sundevall, 1830), other hunters (1258 individuals, 10.13%) comprised largely of *Erigone spp* and *Oedothorax spp* which are separate from other species in the Linyphiidae family due to their versatile hunting strategies, ambush hunters (97 individuals, 0.78%) exclusively from the Thomisidae family and space web weavers (63 individuals, 0.51%) which were all *Robertus lividus* (Blackwall, 1836).

Examining the proportion that each guild contributed to the overall assemblage within each regime showed that the proportion of sheet web weavers was significantly different among grazing regimes ($X^2_{(3, N = 36)} = 15.94$, $p < 0.025$, Bonferroni corrected p values) and was driven by a lower proportion in heavy sheep compared to ungrazed, cattle and light sheep (ungrazed - $z = 3.37$, $p < 0.01$; cattle - $z = 3.53$, $p < 0.001$; light sheep – $z = 3.36$, $p < 0.01$) (Fig. 4). Vegetation structure did not significantly influence the proportion of sheet web weavers among grazing regimes ($X^2_{(1, N = 36)} = 2.97$, $p > 0.025$), though the interaction of grazing and vegetation structure did ($X^2_{(1, N = 36)} = 28.98$, $p < 0.025$). Ground hunter proportion was significantly different among grazing regimes ($X^2_{(3, N = 36)} = 30.16$, $p < 0.014$), though post hoc testing could not find a significant difference among grazing regimes. Examination of data suggests overall model significance may reflect the much lower proportion of ground hunters in heavy sheep regimes compared to the other regimes (Fig. 4). Further, ground hunter proportion was not significantly impacted by vegetation structure or the interaction between grazing and vegetation structure ($X^2_{(3, N = 36)} = 0.99$, $p >$

0.014, $X^2_{(1, N = 36)} = 2.72$, $p > 0.014$). Orb web weaver proportion was not significantly different among grazing regimes after Bonferroni correction ($X^2_{(3, N = 36)} = 3.77$, $p > 0.005$) (Fig. 4) nor was it significant among vegetation structure ($X^2_{(1, N = 36)} = 0.02$, $p > 0.005$) but was significantly different by the interaction of grazing and vegetation structure ($X^2_{(3, N = 36)} = 22.47$, $p < 0.005$). This was driven by a decrease in proportion with increasing vegetation structural complexity in cattle grazing, an increase in proportion with increasing vegetation structural complexity in light sheep and heavy sheep grazing and no change in abundance with increasing vegetation complexity in ungrazed areas (Appendix A3).

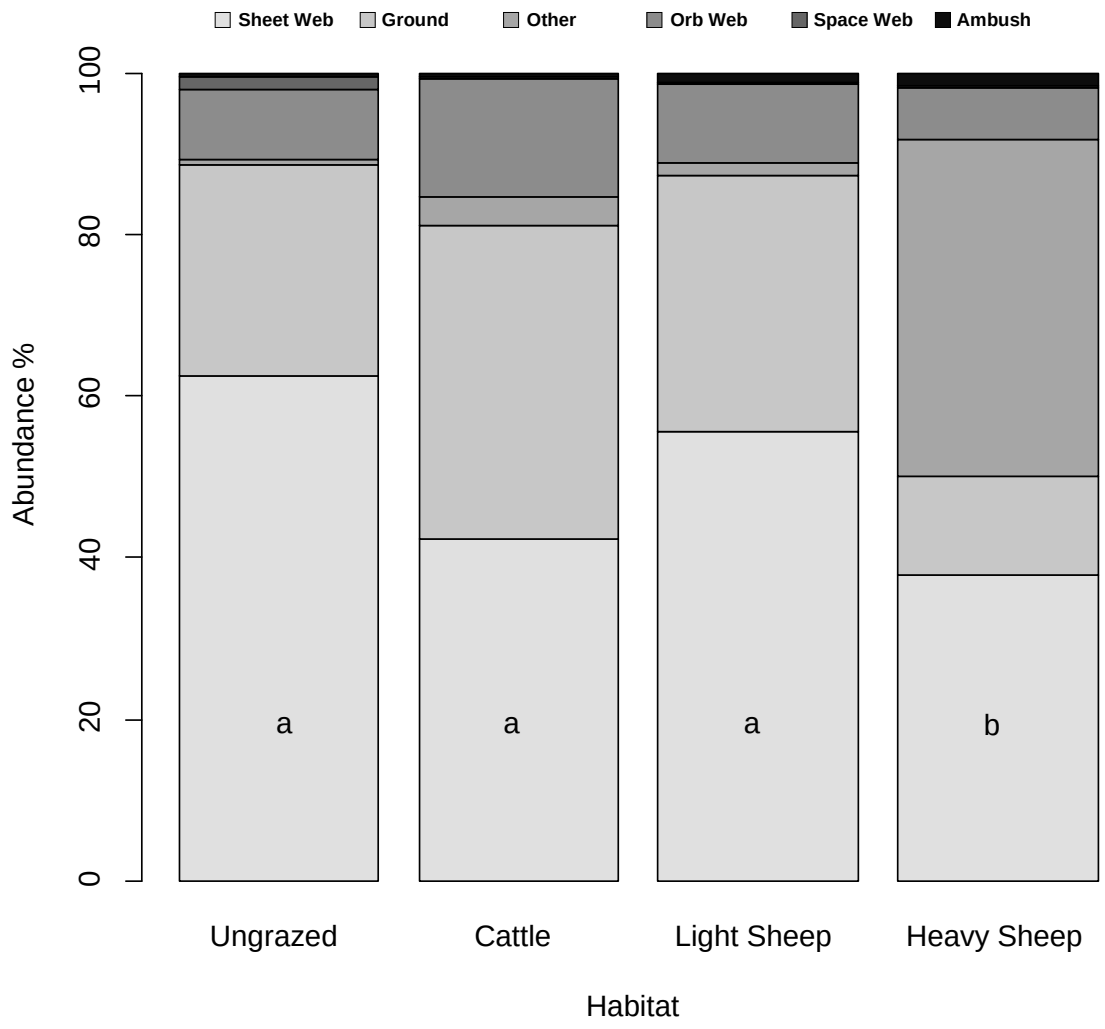

Figure 4 Relative proportion of each guild in each grazing regime. The letters indicate significance of post hoc Tukey, where letters are the different this indicates significant difference ($p < 0.05$).

Spider Assemblages

Spider assemblage differed significantly among grazing regimes ($F_{3, 25} = 7.40$, $p = 0.001$, variation explained = 33.02%), by vegetation structure ($F_{1, 25} = 3.02$, $p = 0.02$, variation explained = 4.51%) and by the interaction of vegetation structure and grazing ($F_{3, 25} = 1.7$, $p = 0.04$, variation explained = 8.12%). The RDA plot (Fig. 5) shows ungrazed and heavy sheep regimes are separated along RDA1. In contrast, cattle and light sheep regimes are not separated from each other and occupy an intermediate position on this axis. Both ungrazed and heavy sheep regimes display a similar spread across RDA2 whereas light sheep and cattle form much tighter clusters.

Indicator species analysis revealed 10 species associated with ungrazed, 10 with heavy sheep, three with cattle and three with light sheep (Table 1). Of the 10 species associated with ungrazed regimes all were from the sheet web weaver guild and either had a habitat preference for leaf litter or humid conditions (Table 1). Six of the 10 species associated with heavy sheep grazing belong to the *Oedothorax* or *Erigone* genera, both of which occupy the 'other' hunting guild category and are associated with short vegetation in highly disturbed habitats (Table 1). Further, the shade intolerant ambush hunter, *Xysticus cristatus* (Clerck, 1757), was also associated with heavy sheep grazing. The three species associated with light sheep grazing were all from the sheet web weaver guild and have a preference for vegetation close to the ground (Table 1). There were three species associated with cattle grazing, one of which was the only ground hunter associated with any of the grazing regimes and is associated with patchy grassland habitats whilst the remaining two were from the sheet web guild.

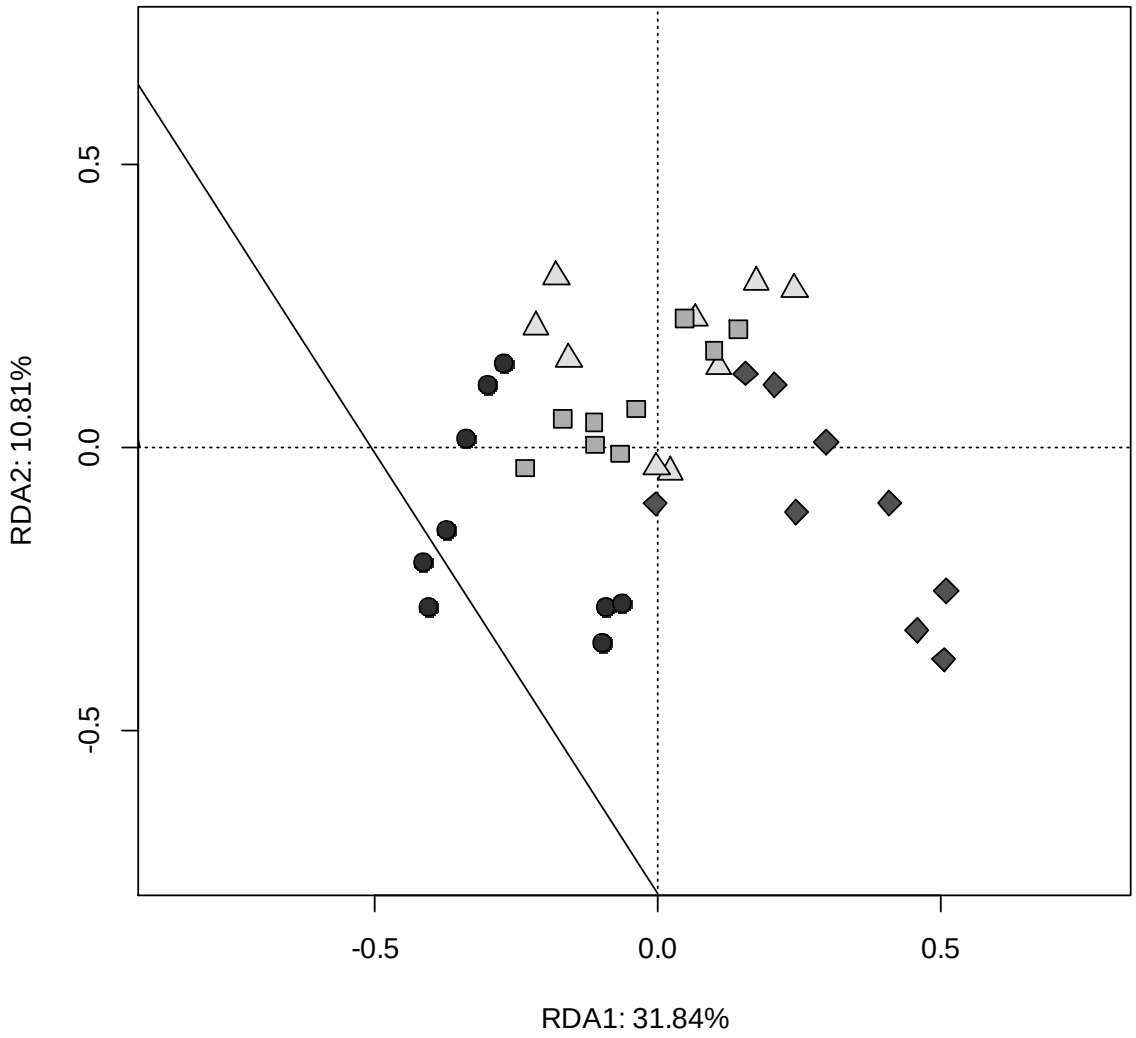

Figure 5 RDA ordination of spider community assemblages by grazing and vegetation structure, and their interaction, constrained by geographical location. The percent of variation explained by each RDA axes after removing the contribution of site is: RDA1 is 31.84% and by RDA2 is 10.81%. Circles = ungrazed; triangles = cattle; squares = light sheep; diamonds = heavy sheep.

Table 1: Spider species associated with grazing regime. Indicator Species Analysis produces an Indicator Value between 0 – 1, with values closest to 1 signifying a perfect indictor (always present in a particular treatment and exclusive to that treatment). P values signify significance of Indicator Values for each species based on Monte Carlo randomisation procedure with 4999 iterations. Hunting guilds were gathered from Cardoso *et al.* (2011) and habitat preferences gathered from Harvey *et al.* (2002). All species were categorised as of least concern in Britain by Dawson *et al.* (2008). GH = ground hunter; SW = sheet web weaver; OP = space web weaver; AM = ambush hunter. $p< 0.05$ = *; $p < 0.01$ = **; $p< 0.001$ = ***.

	Family	Guild	Habitat Preferences	Indicator Value
Ungrazed				
Monocephalus fuscipes	Linyphiidae	SW	Litter in woodland but also in grassland	0.62^{***}
Robertus lividus	Theridiidae	SP	Leaf litter	0.60^{**}
Palliduphantes pallidus	Linyphiidae	SW	Litter and under stones	0.56^{**}
Pocadicnemis pumila	Linyphiidae	SW	Grassland, moorland, blanket bog (damp conditions)	0.53^{***}
Saaristoa abnormis	Linyphiidae	SW	Leaf litter	0.51^{**}
Palliduphantes ericaeus	Linyphiidae	SW	Amongst plant stems, litter, require humid conditions	0.50^{**}
Bathyphantes parvulus	Linyphiidae	SW	Grasslands, also marshes and fens	0.46^{*}
Walckenaeria acuminata	Linyphiidae	SW	Damper substrates, any habitat in the ground zone	0.44^{*}
Micrargus apertus	Linyphiidae	SW	Litter	0.33^{*}
Centromerus dilutus	Linyphiidae	SW	Detritus	0.32^{*}
Cattle				
Gongylidiellum vivum	Linyphiidae	SW	Grassland, damp situations	0.44^{*}
Pardosa pullata	Lycosidae	GH	Grassland with tussocks	0.44^{*}
Silometopus elegans	Linyphiidae	SW	Grass, wet or marshy places	0.38^{*}

Light Sheep				
Hahnia nava	Hahniidae	SW	Moss and other low vegetation and amongst stones	0.63***
Agyneta cauta	Linyphiidae	SW	Litter, detritus, occasionally moss on damp sites	0.46*
Peponocranium ludicrum	Linyphiidae	SW	Unimproved grassland, close to the ground.	0.44*
Heavy Sheep				
Erigone atra	Linyphiidae	O	Low vegetation – ubiquitous	0.77***
Bathyphantes gracilis	Linyphiidae	SW	Grasslands – ubiquitous	0.69***
Oedothorax retusus	Linyphiidae	O	Grassland and agricultural fields	0.65**
Dicymbium tibiale	Linyphiidae	SW	Under stones	0.63**
Oedothorax gibbosus	Linyphiidae	O	Moist/disturbed habitats	0.56**
Oedothorax fuscus	Linyphiidae	O	Short grassland	0.55**
Xysticus cristatus	Thomisidae	AM	Disturbed grasslands, shade intolerant	0.47*
Erigone dentipalpis	Linyphiidae	O	Low vegetation – ubiquitous	0.45*
Tiso vagans	Linyphiidae	SW	Grassland - aeronaut	0.43*
Oedothorax agrestis	Linyphiidae	O	Saturated habitats	0.33*

Discussion

This study found that the spider fauna of upland calcareous grasslands is influenced by both grazing type and vegetation structural complexity, and that the impacts of vegetation structure are not consistent among the regimes. The distinct spider assemblages in ungrazed and heavy sheep grazed regimes reflects the interaction of grazing and structural complexity and is in concordance with experimental studies from a lowland calcareous grassland and upland *Nardus stricta* grasslands which examined the impacts of vegetation height on spiders (Gibson *et al.* 1992; Dennis *et al.* 2001). The overlap in assemblage between light sheep and cattle grazed regimes in the current study is reflective of the comparative structural complexity in these regimes, suggesting the differences in assemblage are influenced more by grazing intensity than the type of grazing animal used. The contrasting assemblages among grazing regimes can be accounted for by the response of spider species to vegetation structure. Six of the ten species associated with ungrazed regimes in this study (Table 1) are acknowledged as having habitat preferences for plant litter (Harvey at al. 2002). The greater amount of plant litter (in this case thatch) in ungrazed regimes provides increased refuges for spiders (Rypstra *et al.* 1999). Structural differences in vegetation influences microhabitat conditions such as humidity, which in turn influences the distribution of some spider species (Bell *et al.* 2001; Almquist, 1973). For example, greater structural complexity from ungrazed vegetation provides a more stable and humid microclimate than grazed vegetation by protecting from extreme climatic conditions (van Klink *et al.* 2015; Pétillon *et al.* 2010; De Keer *et al.* 1989). The combination of high structural complexity and a well-developed layer of thatch may be particularly important for maintaining a stable microclimate in free draining upland calcareous grasslands, especially where temperatures can range from below freezing to

over 20°C in the summer months. In the present study, six of the ten species that had strong associations with ungrazed regimes have preferences for damp/humid conditions (Table 1). In addition, all the indicator species of the ungrazed regime are sheet web weavers, which capture prey on small webs laid over or amongst vegetation. This suggests that the lack of disturbance by livestock in ungrazed areas shapes assemblages by providing a structurally stable habitat and microclimate.

By comparison, the reduced structural complexity and reduced proportion of thatch of the heavy sheep grazed regime provides conditions for species associated with short vegetation and good dispersal abilities which are well known from disturbed habitats e.g. *Erigone atra* Blackwall, 1833, *Oedothorax fuscus* (Blackwall, 1834), *Tiso vagans* (Blackwall, 1834) (Duffey, 2005; McFerren *et al.* 1994). Spider assemblages in heavy sheep grazing have been referred to as pioneer (Duffey, 1993), consisting of species that are active aeronauts, able to disperse freely and exploit open ground where competition is low. The reduced potential web anchorage points due to low structural complexity favour the versatile foraging strategies of *Erigone* and *Oedothorax* species (Alderweireldt, 1994). Six of the ten species associated with this regime belong to either of these genera, all of which are in the 'other' hunting guild. This guild constitutes the greatest proportion of all guilds in heavy sheep grazing and is proportionally greater than in all other regimes. It is comprised of species with varied and often versatile hunting strategies which may help survival in highly disturbed habitats e.g. *Erigone* species may vary their mode of foraging between actively catching prey and capturing prey in a small web which is not reliant on tall vegetation but is usually constructed very close to the surface of the ground (Maelfait and De Keer, 1990; Alderweireldt, 1994). The association of the shade intolerant ambush hunter *X. cristatus* which can adopt a hunting position on the ground surface, thus not

relying on complex vegetation, also reflects the influence of reduced vegetation structural complexity and low levels of thatch present in this regime (Harvey *et al.* 2002).

The reduced structural complexity in heavy sheep grazing also accounts for the reduced proportion of the ground hunter guild compared with other grazing regimes. Ground hunters, such as those in the genus *Pardosa*, require increased structural complexity as they utilise different aspects of the vegetation in different life stages (Vlijn and Kessler-Geschiere, 1967). *Pardosa* species use open patches to search for prey or copulation partners by sight, females utilise sites exposed to sunlight to warm their cocoons and juveniles seek refuge in taller vegetation to overwinter (Bristowe, 1958; De Keer et al, 1989; Malfait and De Keer, 1990). The present study suggests intermediate structural complexity promotes increased spider abundance, as evidenced by the greater abundance in cattle grazing than heavy sheep grazing. Here, the interaction of grazing and vegetation structural complexity may be important and as demonstrated by the association of *Pardosa pullata* (Clerck, 1757), which was found in much greater abundance in cattle grazing (30% of total spiders in this regime), than heavy sheep grazing (6% of total spiders in this regime). The greater disturbance in heavy sheep regimes as a result of increased grazing pressure resulted in structural homogeneity. This is in contrast with the heterogeneous structure of light cattle grazed regimes which result from reduced grazing pressure. Under this reduced grazing pressure structural complexity increases as stock are able to avoid unpalatable vegetation (e.g. around dung, less favoured plants etc.) which creates more niches (Grant *et al.* 1985; Maelfait and De Keer, 1990; Woodcock *et al.* 2009). Indeed, Maelfait and De Keer (1990) found that juvenile *Pardosa palustris* (Linnaeus, 1758) utilised taller vegetation growing around cattle dung as overwinter refuge. The disturbance activity at reduced grazing levels creates heterogeneity, and thus more niches, in the

vegetation structure through vertical niche differentiation (Denno, 1980). In comparison, few niches are available in heavy sheep regimes as a result of reduced, and more homogenous, vegetation structural complexity.

In the present study grazing regime affected heterogeneity of vegetation structural complexity. Vegetation structure was heterogeneous in ungrazed, light cattle and light sheep regimes whilst structure in heavy sheep regimes was homogeneous. Though vegetation structure was heterogeneous in light cattle, light sheep and ungrazed regimes, the latter was distinct in having greater overall structural complexity. This is reflected in differences in spider abundance among these regimes which is greater in light cattle and light sheep compared with ungrazed (Fig. 3). This is contrary to previous experimental studies on spider abundance in relation to stocking densities similar to those in this study, which found spider abundance increased with decreasing stocking densities 12-18 months after changes in grazing regime (Dennis *et al.* 2015; Mysterud at al. 2010). Further, whilst assemblages differed amongst grazing regimes this was driven by changes in composition and abundance rather than spider species richness, where similar numbers of spider species were supported amongst the grazing regimes in upland calcareous grassland. This contrasts with the observation of greater species richness with reduced stocking density reported by Dennis *et al.* (2015) and Mysterud *et al.* (2010) in other grassland habitats, though the former conceded that the period of equilibrium following changes in grazing practices needed further investigation. In the present study, grazing had been in place for a minimum of 10 years prior to sampling. The contrasting results of spider abundance and richness in the present study compared to those of Dennis *et al.* (2015) and Mysterud *et al.* (2010), where grazing was in place for only three years and one year prior to investigation

respectively, may reflect adequate time for equilibrium to be reached in upland calcareous grasslands.

Conservation significance and management recommendations

In this study vegetation structural complexity did not increase with greater plant species richness but instead responded to grazing intensity, as observed in ungrazed regimes. Further, spider species richness did not differ among grazing regimes, but spider assemblage, guild proportion and presence of rare species did, likely due to differences in vegetation structural complexity and disturbance. Therefore, it is recommended that management decisions include the consideration of maintaining varied structural complexity to support a diverse spider community across the landscape.

The intermediate structural complexity of light sheep and cattle grazing produces a distinct assemblage and greater abundance than high intensity sheep grazing and no grazing. The latter possibly being driven by the success of *P. pullata*. Further, ungrazed regimes provide a unique habitat, with high structural complexity and increased thatch layer, which produces a distinct spider assemblage consisting of species that require a specific microclimate as indicated by the association of species with habitat preferences for high humidity. Given the scarcity of ungrazed grasslands and the length of time taken to produce its structural complexity, coupled with the presence of the endangered *P. egeria* and *J. falconeri* and the vulnerable *A. subtilis*, *W. dysderoides*, *W. inscisa* and *W. obtusa*, the continuation of this regime is recommended.

The distinct assemblage in heavy sheep grazing reflected a community of commonly found disturbance tolerant pioneer species, with little in common with the diverse assemblages that could be supported by lighter grazing regimes. Though *J. falconeri*, *A. subtilis* and *W.*

dysderoides were recorded in heavy sheep grazing they were not exclusive to this treatment and as this grazing regime is common across the landscape, the cessation of heavy sheep grazing on internationally important calcareous grassland is recommended. Spider assemblages were comparable between light sheep and cattle grazing, and both support *J. falconeri*, *A. subtilis*, *W. dysderoides*, and *W. inscisa*. However, since a few vulnerable spiders were only found with cattle (*A. scopigera*, *M. minutus* and *T. thorelli*) or light sheep (*W. monoceros*) there is a strong argument for the continuation of both grazing types across the landscape.

Chapter 4

Epigeal spider diversity of habitats associated with the upland calcareous grassland matrix

Prepared for submission to *Insect Conservation and Diversity*

Abstract

1. Upland calcareous grassland landscapes are typically comprised of a matrix of calcareous grassland, acid grassland and limestone heath plant communities. This matrix of habitats is produced by a combination of underlying geology, climate and management.

2. Upland calcareous grassland landscapes are typically managed through grazing, with management targeted to maintain particular plant communities in the calcareous grassland habitat, whilst patches of acid grassland and limestone heath are not targeted by conservation management.

3. The biodiversity value of acid grassland and limestone heath patches within the calcareous grassland matrix are unknown. This study provides the first assessment of their biodiversity value by examining aspects of epigeal spider diversity supported by these non-target habitat patches in comparison to calcareous grassland.

4. Spider species assemblages were distinct between limestone heath and both grassland types. Distinction in species assemblages are likely due to differences in vegetation structure and microclimate e.g. humidity, degree of shade.

5. Each habitat type supported several unique rare species (e.g. *Porrhomma egeria* in limestone heath, *Trichopternoides thorelli* in acid grassland and Walckenaeria

monoceros in calcareous grassland) revealing the contribution of each habitat type to spider fauna.

6. The distinct spider species assemblage and presence of rare species in limestone heath patches demonstrate their importance in the upland calcareous grassland matrix. The introduction of management for some of these patches is recommended to promote early successional stages of heather which may be beneficial for the conservation of a number of notable spider species.

Key words: Heath; Acid grassland; Conservation; Assemblage; Beta diversity; Sheep; Management.

Introduction

Calcareous grassland, considered among the most species rich and diverse habitats for many species groups in Europe, underwent wide scale loss and degradation following post 1950s agricultural intensification and as such has become the focus of conservation efforts (Willems, 2001; Fischer and Stocklin, 1997; Poschlod *et al.* 2005; Poschlod and Wallis de Vries, 2002; Roesch *et al.* 2013; Wallis De Vries *et al.* 2002). Afforded protection under Annex I of the EU habitats directive, an estimated 595 973 ha is protected in the Natura 2000 network across EU member states (Calaciura & Spinelli 2008). Their management typically aims to maintain particular plant communities through prevention of succession and domination by one or few species (Willems, 2001; Wallis de Vries *et al.* 2002).

In upland regions of the UK, high stocking densities of sheep were implicated as a major cause of habitat deterioration and the decline of associated plants, invertebrates and birds (Dennis *et al.* 2008; Fuller & Gough, 1999). In an attempt to conserve the characteristic vegetation of rare upland calcareous grassland, which covers just 0.1% (22000-25000ha) of total UK land cover (calculated from Maddock, 2008; DEFRA, 2013), there has been a reduction in stocking levels within the last decade.

Upland calcareous grassland landscapes are typically comprised of a matrix of calcareous grassland, acid grassland and limestone heath plant communities. This matrix of habitats is produced by a combination of underlying geology, climate and grazing management (Rodwell, 1992; Rodwell *et al.* 2007). Thin, well drained, lime rich soils found on limestone bedrocks provide suitable conditions for calcareous grassland (Rodwell *et al.* 2007; Joint Nature Conservation Committee, 2007). Superficial deposits of glacial till or

loess among the thin soil overlying the limestone bedrock produce patches of plant communities within the calcareous grassland which are dominated by calcifuge species (Rodwell, 1992; Dixon, 1982). Under reduced intensity sheep grazing, these patches are either maintained as acid grassland (dominated by *Nardus stricta*) or develop into the climax community of limestone heath (EC Habitats Directive Annex 1 (Joint Nature Conservation Committee, 2013)). The selective grazing behaviour of sheep results in particular vegetation patches experiencing different effective stocking densities (Dennis *et al.* 2015; Grant *et al.* 1985). At low stocking densities sheep restrict grazing to vegetation patches containing preferred plant species resulting in effectively ungrazed patches of less preferred vegetation (Hester and Baillie, 1998). Thus a combination of underlying geology and management produces a mosaic of habitats within the calcareous grassland matrix, adding heterogeneity to the landscape.

Little is known about the biodiversity value of these habitat patches in the calcareous grassland matrix. While the calcareous grassland itself is recognised as a priority habitat for conservation and targeted by conservation management, the value of patches of limestone heath and acid grassland in the grassland matrix is often overlooked, and not targeted by management, despite the former being included under Annex 1 of the EC Habitats Directive (Joint Nature Conservation Community, 2013). Such habitats outside of the calcareous grassland matrix are known to support distinct plant and animal assemblages (Dennis et al, 2001; Littlewood *et al.* 2006).

Invertebrates are potentially good indicators of biodiversity, with important roles in food web dynamics, acting as predators, prey and decomposers (Vickery *et al.* 2001; Voigt *et al.* 2007). Further, they are influenced by disturbance and by microclimate which alters with

vegetation structural complexity (Cole *et al.* 2010; Kruess and Tscharntke, 2002; Woodcock and Pywell, 2010). Spiders play an important role in the functioning of all ecosystems, occupying an important role in terrestrial food webs as both predators and prey (Turnbull, 1973; Uetz, 1991). They encompass a wide range of foraging strategies and as such are differentially sensitive to variations in vegetation architecture and disturbance (Chapter 3, this thesis; Barriga *et al.* 2010; Diehl *et al.* 2013; Gibson *et al.* 1992). Differences in foraging strategies are linked to vegetation structure and disturbance (Chapter 2, this thesis; Alderweireldt, 1994; Bell, *et al.* 2001; Uetz, 1991). Ground hunting species require a heterogeneous sward of open patches to search for prey and taller vegetation for refuge (Malfait and De Keer, 1990), whereas orb web weaving spiders select structurally complex vegetation that provides increased web anchorage points (Diehl *et al.* 2013; Langellotto and Denno, 2004; McNett and Rypstra, 2000). The differences in foraging strategy, activity and substrate utilisation amongst species make grouping spiders into guilds a useful tool for examining functional differences among habitats (Corcuera *et al.* 2015; Schweiger *et al.* 2005). It would be expected that the contrasting structure and differences in relative stocking densities of the non-target habitats in the calcareous grassland matrix will impact both potential niche availability and microclimate e.g. humidity and temperature stability, thus providing conditions suited to different species or hunting guilds.

Furthermore, spider diversity correlates with total arthropod diversity over a wide range of cultivated habitats in Central Europe (Duelli & Obrist, 1998). Thus, their ecological requirements and relationship with other taxa make them a useful group for studying differences in diversity among contrasting habitat types.

This study is the first to investigate the biodiversity value of non-target habitats within the upland calcareous grassland matrix, using spiders as a model group. Specifically, it will ask:

1. How do spider assemblages differ among habitats in the upland calcareous grassland matrix?

2. How does functional diversity, measured by hunting strategy, differ among habitat types in the matrix?

3. Do non-target habitats support species of conservation interest?

Methods

Study Sites

Three sites of extensive areas of calcareous grassland (size 35ha – 525ha, median 76ha) were selected for study across geographically distinct regions separated by 14-48km in Northern England (54°29′44.41″N, 002°33′20.03″W) (54°09′03.76″N, 002°06′00.29″W) (54°08′44.37″N, 002°19′17.54″W). Each study site was under the same management of sheep grazing with a stocking intensity of <0.24 LU ha^{-1} yr^{-1} that had been in place for a minimum of ten years prior to study. Elevation ranged from 213 – 383m, median 355m. Soil across the sites was generally base rich with some deposits of glacial till and peat resulting in each site containing three habitat types: a matrix of calcareous grassland, targeted by conservation management, along with scattered patches of *Nardus stricta* grassland and limestone heath, both non-target habitats. The habitats were defined as: calcareous grassland which had a species rich sward with a mean sward height of 8.09cm over the sampling period, limestone heath which occurred in patches exceeding $20m^2$ and was dominated by mature stage *Calluna vulgaris*, and acid grassland which was dominated by *Nardus stricta*, and again occurred in patches exceeding $20m^2$. In addition, though vegetation height in acid grassland and heath was not measured there was an observable distinction in vegetation height between both grassland types and heath, the canopy of which always exceeded 30cm. Further, the ground layer of heath largely lacked vegetation, instead having a covering of heather litter. In contrast, both the calcareous grassland and acid grassland had a well-developed ground layer, with the acid grassland having dense tufts of *N. stricta*.

Three representative samples of each habitat type were selected as replicates at each study site. Each habitat replicate was spaced a minimum of 51m (median 226m) from other replicates to ensure statistical independence of samples (Digweed *et al.* 1995), and a minimum of 50m away from disturbance e.g. footpaths, water troughs etc. Spatial independence of samples was confirmed with Moran's I based on nearest neighbour distances for all 27 locations for spider abundance (Moran's I ± SD: -0.06 ± 1.14, p = 0.87) (Bivand *et al.* 2014). Within each site, collections of epigeic spiders were conducted between May – August 2014.

Spider Sampling

Within each habitat replicate, six pitfall traps, spaced 2m apart, were established to capture spiders. Traps consisted of a plastic cup approximately 7cm in diameter and 9cm deep and covered with a square plastic lid suspended 1cm from the ground by pegs to prevent rain water and debris from entering. These were filled to 1cm depth with antifreeze to act as a killing and preserving agent. To prevent traps being trampled or interfered with by livestock each trap was protected by a secured cage made from 2.5cm x 2.5cm gauge mesh. These cages do not affect the trapping rates of ground-dwelling invertebrates (Oxbrough *et al.*, 2012). Where traps were set in patches of acid grassland or limestone heath they were placed in the centre of the patch, where they were set in calcareous grassland they were placed a minimum of 50m from other habitat types. Traps were set between 05/05/2014 and 21/08/2014 and were changed every 21 days, giving a total of 105 trap days. Samples from five of the traps within each location were pooled for analysis. All adult spiders were identified to species level using Roberts (1993) and nomenclature follows World Spider Catalogue (2017). Since it was not possible to reliably identify most juvenile species these were excluded from the study. Information on conservation status

was gathered from Dawson *et al.* (2008). Spider reference specimens are housed at the Edge Hill University Department of Biology arthropod collection.

Spider Hunting Guilds

Following identification to species, spiders were separated into six hunting guilds based on hunting strategies suggested by Cardoso *et al.* (2011): sheet web weavers, ground hunters, space web weavers, orb web weavers, ambush hunters and other hunters. The list of spider species and associated guilds is included in Appendix A4.

Data Analysis

Five of the pitfall traps in each habitat replicate were pooled across the full sampling period. To account for differences in trapping effort all samples were standardised to trap day by calculating the abundance of each species at each location and dividing it by the number of actual trap days at that location and then multiplying it by the maximum number of trap days across all locations (105), a standard method used in studies using pitfall trapping (Bergeron *et al.* 2013; Blanchet *et al.* 2013: Pinzon *et al.* 2013).

Statistical analyses were carried out with R statistical software (version 3.2.0.) (R Core team, 2015) and EstimateS (version 9.1.0) (Colwell, 2013).

Raw spider species data (not standardised by trap day) was used to examine differences in species richness among habitats using sample based rarefaction calculated using EstimateS, version 9.1.0 (Colwell, 2013) with rarefaction curves produced in R and scaled by the number of individuals. This technique accounts for differences in sampling effort by standardising species richness for the number of individuals within a sample. Rarefaction

estimates the number of species expected in a random sub-sample extracted from a larger sample (Chao, 2005; Magurran, 1988, 2004).

Differences in spider abundance among habitat types were examined with Generalised Linear Mixed Models (GLMMs) performed with negative binomial errors using the glmer function of the lme4 package (Bates *et al.* 2015). Habitat was modelled as a fixed factor with region modelled as a random factor. Negative Binomial errors were used to combat overdispersion of Poisson errors (dispersion = 43.82) (Thomas, 2017). The model was tested for significance using the Anova function of the Car package (Fox and Weisberg, 2011) and post hoc Tukey pairwise comparisons were used to test for differences among grazing regimes, correcting p values for multiple comparisons with the Holm method using the glht function of the multcomp package (Hothorn *et al.* 2008).

The comparative proportion of each hunting guild among habitats was compared using GLMMs computed with Binomial errors. Habitat was modelled as a fixed factor and region modelled as a random factor. GLMMs were computed for ground hunters, sheet web weavers and orb web weavers. Space web weavers, ambush hunters and other hunters were not examined in this way as the abundance of each groups was too small and contained too many zero observations. Each model was tested for overdispersion of Binomial errors (dispersion: ground hunters = 13.72; sheet web weavers = 9.77; orb web weavers = 26.41). To correct for overdispersion, observation level random effects were included in the overall model (Harrison, 2014). Bonferonni correction was applied to the confidence intervals to account for the multiple testing of the abundance data (e.g. split into six guilds). However, as the number of species was not divided equally among the six guilds the confidence intervals at which statistical significance was determined using the

Bonferonni correction were not set at equal (e.g. 0.05/6) but rather as the proportion that each guild comprised of the data set (required confidence intervals to infer significance: ground hunters < 0.014; sheet web weavers < 0.028; orb web weavers < 0.006) following Neuwald and Green (1994).

Spider species composition was examined through Redundancy Analysis (RDA) computed on Hellinger transformed spider species data using the RDA function in the vegan package in R (Oksanen *et al.* 2016). Habitat was included as the main term in the model with region included as a random factor. Permutation test, with 9999 permutations, was used to test final significance of the model.

Beta diversity (β), defined as variability in spider species composition (Anderson *et al.* 2006), among habitats was quantified using the betadisper function in the vegan package in R (Oksanen *et al.* 2016), followed by permutation test (999 permutations) to test for significance. betadisper measures β diversity by assessing the variability in average distances from the group centroid among individual sampling units (Anderson *et al.* 2006). The analysis was conducted on spider species data transformed into a dissimilarity matrix calculated with the Simpson dissimilarity index ($_{bsim}$) (Koleff *et al.* 2003). Simpson dissimilarity index is appropriate for use in this instance as it measures differences in species composition independent of richness gradients (Baselga, 2007; Koleff *et al.* 2003). The dissimilarity matrix is presented graphically in a Principal Coordinate Analysis (PCoA) plot based on group centroids.

Significant associations of spider species with each habitat type were determined using indicator species analysis (Dufrene and Legendre, 1997) using the indval function of the

labdsv package (Roberts, 2015). Indicator Species Analysis produces indicator values between 0 – 1, a value of 1 represents a perfect indicator that is always present in a particular treatment and is exclusive to that treatment (McCune *et al.* 2002). Significance of indicator values was assessed using a Monte Carlo randomisation procedure with 4999 iterations. Significant indicator values infer species associations with each habitat type as a mechanism to characterise habitat use by spiders.

Results

A total of 12 878 individual spiders from 89 species were collected. 4066 (31.57% of overall abundance) of these were juveniles and 103 (0.80%) were damaged specimens. Neither of these groups could be identified and were therefore omitted from the data set. A total of 8709 individuals from 89 species of nine families representing six hunting guilds were included in the following analyses. A full list of species is given in Appendix A4. Overall, only three species individually made up more than 5% of the total spider abundance, together totalling 29% of the overall catch: *Pardosa pullata* (Clerk, 1757) (14.13%), *Pachygnatha degeeri* Sundevall, 1830 (8.24%) and *Silometopus elegans* (O. Pickard-Cambridge, 1873) (6.88%).

Spider diversity

Rarefaction curves showed that spider species richness did not differ among grazing treatments (Fig. 1), as indicated by the overlap in confidence intervals. Spider abundance was different among habitats ($X^2_{(2, N = 27)} = 9.69$, $p < 0.01$), with greater abundance in acid grassland and calcareous grassland compared with heath ($z = 2.65$, $p < 0.05$; $z = 2.71$, $p < 0.05$ respectively) (Fig. 2).

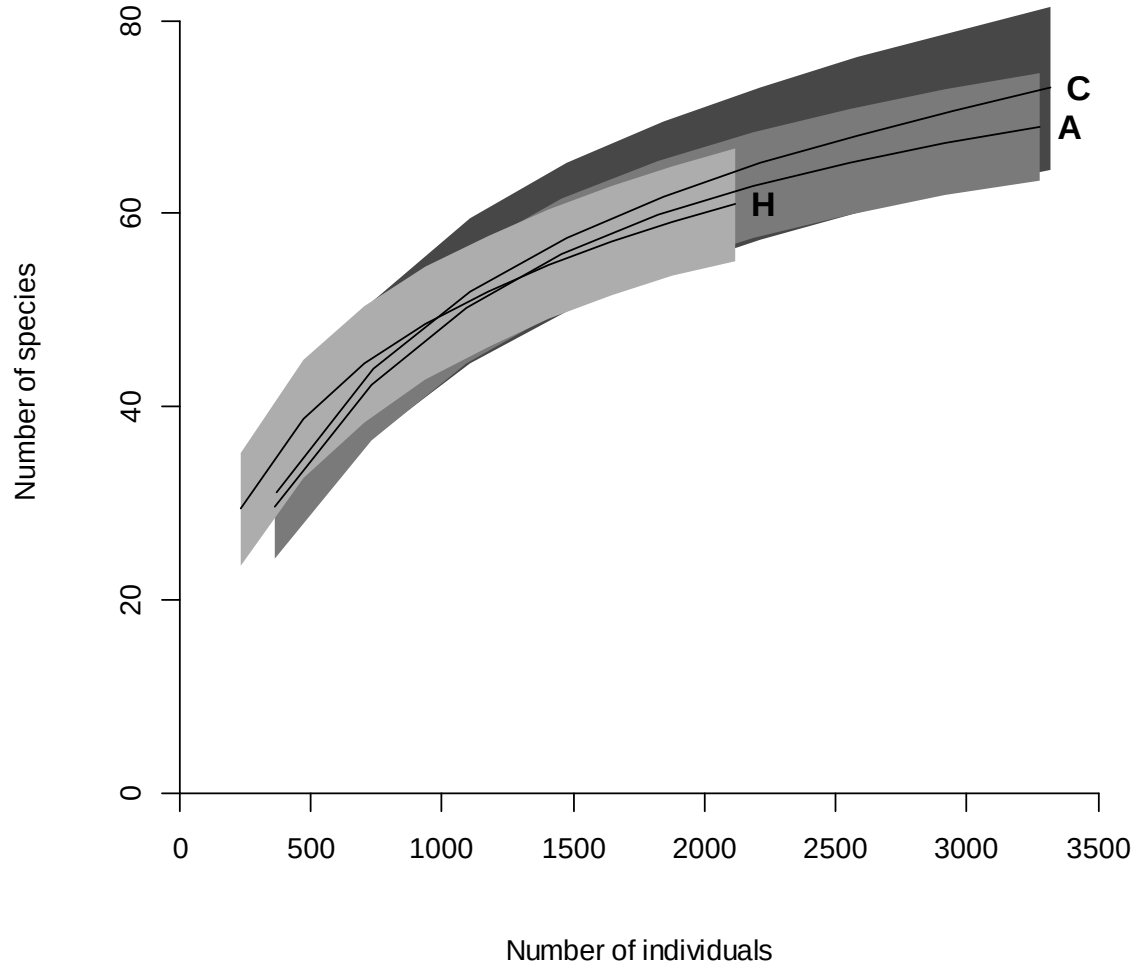

Figure 1 Sample based rarefaction curves scaled by the number of individuals, indicating spider species richness. A = acid grassland, C = calcareous grassland, H = heath. Grey bars indicate 95% confidence intervals

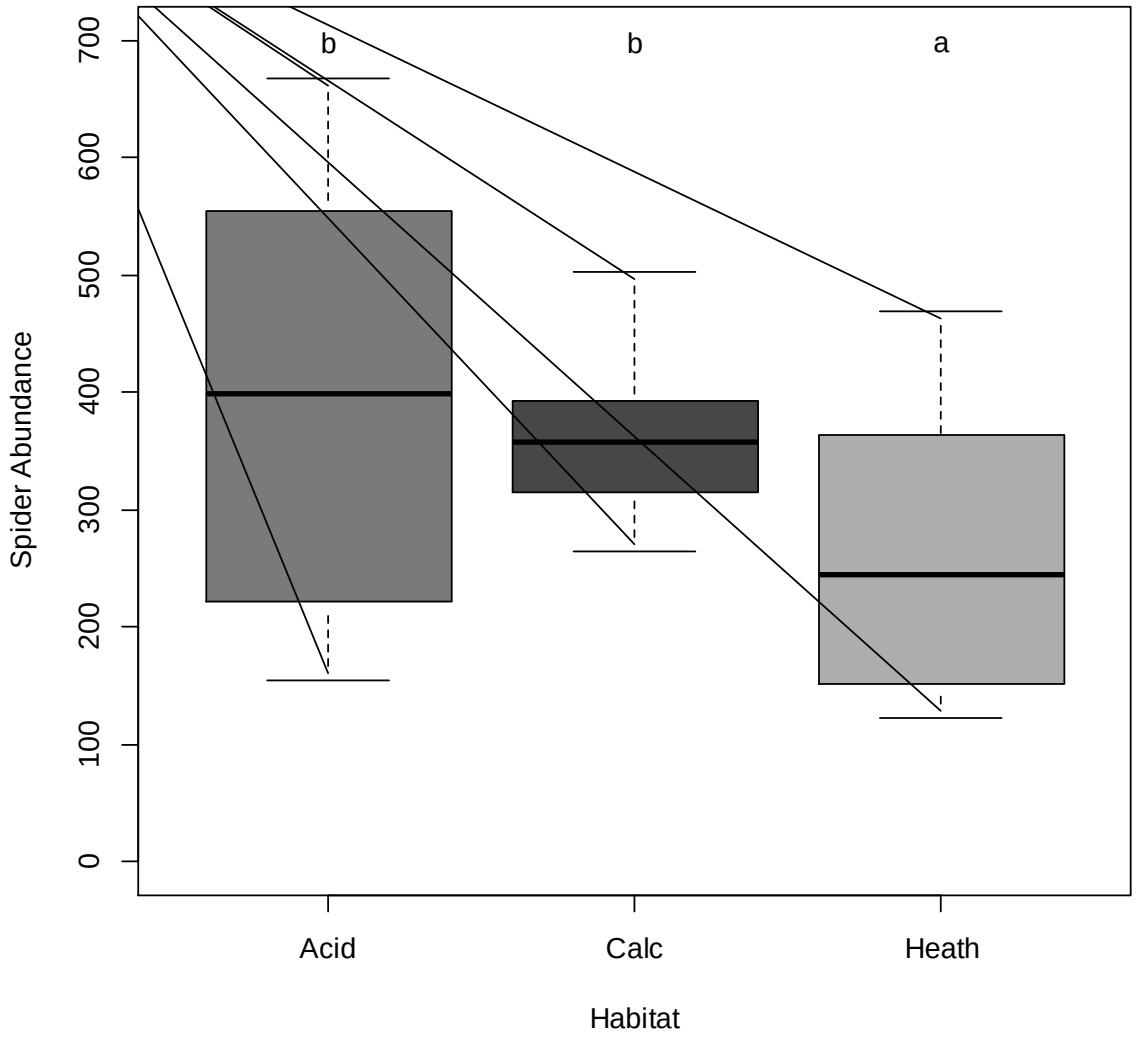

Figure 2 Spider abundance among habitat types. The letters indicate significance of post hoc Tukey test, where letters are different this indicates a significant difference ($p < 0.05$).

How do spider assemblages differ among habitats in the calcareous grassland matrix?

Spider species assemblage differed significantly among habitats ($F_{2, 22} = 5.40$, $p = 0.001$) which accounted for 26.32% of the variability in the overall model. The conditional variable of region accounted for 20.08% of the variability in the overall model. The first two RDA axes accounted for 32.92% of the variation in the model after the contribution of region was removed (Fig. 3). The contribution of RDA axis one to the variation in the model was significant ($F_{1, 22} = 8.77$, $p = 0.001$) and represents a separation of heath from both acid grassland and calcareous grassland (Fig. 3). RDA2 distinguishes acid grassland from calcareous grassland, however, this axis was not significant ($F_{1, 22} = 2.03$, $p = 0.081$).

β diversity was significantly different among habitat types ($F_{2, 24} = 4.95$, $p = 0.02$). Significant differences were found in the pair wise comparisons of the habitats acid grassland and heath ($p = 0.043$) and calcareous grassland and heath ($p = 0.008$), but not calcareous grassland and acid grassland ($p > 0.05$). The PCoA plot (Fig. 4) shows distinct separation of heath from both acid grassland and calcareous grassland on PCoA1 indicating a difference in β diversity. Further, both acid grassland and calcareous grassland overlap on both axes indicating no difference in β diversity. The greater spread of both acid grassland and calcareous grassland along both axes compared to heath indicates greater β diversity in both of the former compared to the latter.

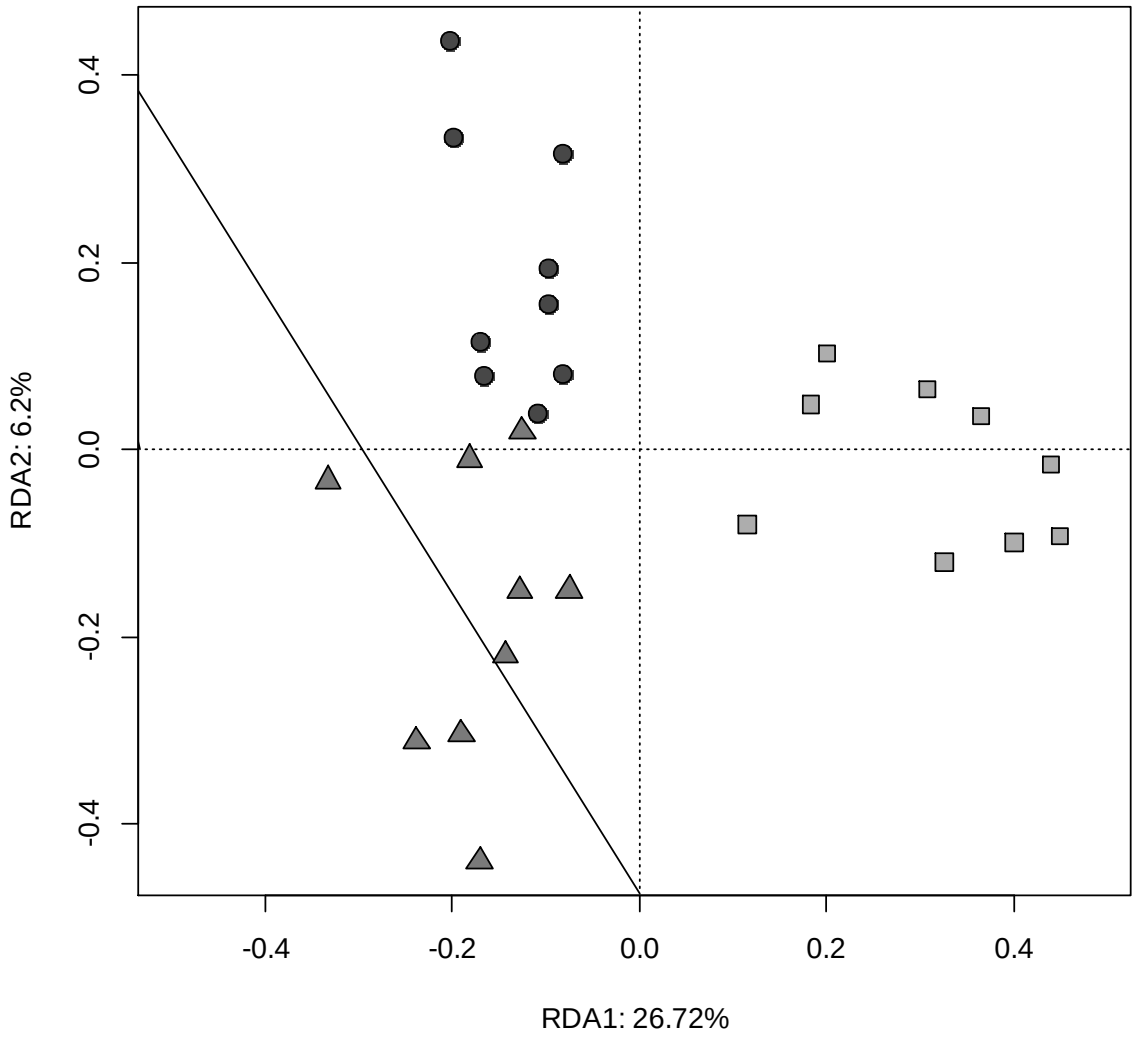

Figure 3 RDA of spider assemblage by habitat type. Region partialled out. Variation in the model represented by RDA1 was significant ($F_{1, 22} = 8.77$, $p = 0.001$) whilst RDA2 was not significant ($F1_{, 22} = 2.03$, $p = 0.081$). Circles = calcareous grassland, triangles = acid grassland, squares = heath.

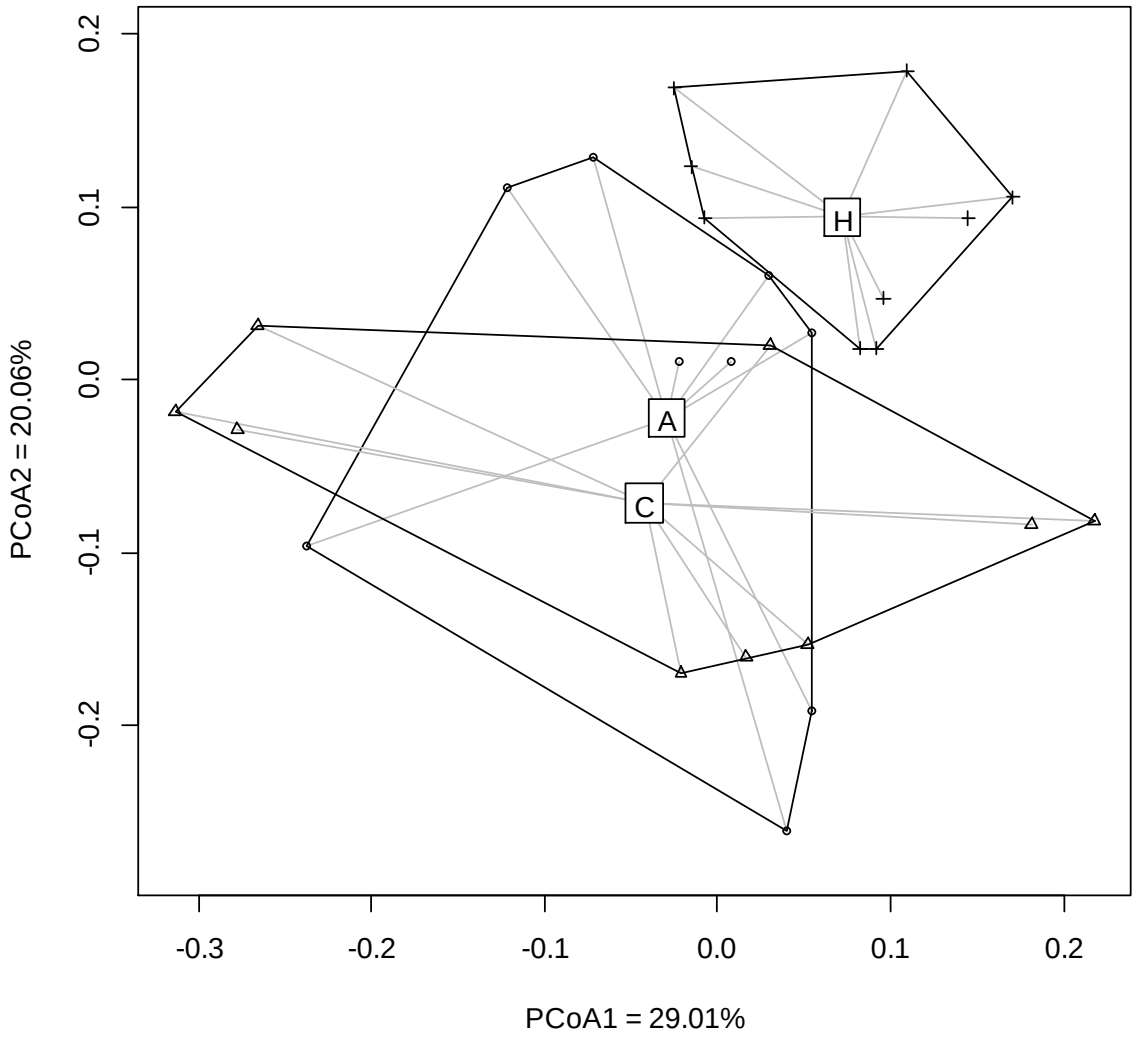

Figure 4 Principal Coordinate Analysis plot showing average dissimilarity from individual observations to their group centroids. H = heath, A = acid grassland, C = calcareous grassland. Permutation test: Heath – acid grassland p = 0.04, heath – calcareous grassland p = 0.004, acid grassland – calcareous grassland p = 0.54.

How does functional diversity, measured by hunting strategy, differ among habitat types in the matrix?

The most abundant guild was sheet web weavers (5233 individuals, 56.03%), then ground hunters (2643 individuals, 28.30%), orb web weavers (1140 individuals, 12.21%), other hunters (166 individuals, 1.78%), space web weavers (100 individuals, 1.07%) and ambush hunters (58 individuals, 0.62%).

The proportion of sheet web weavers was significantly different among habitats ($X^2_{(2, N = 27)} = 77.44$, $p < 0.028$) (based on Bonferroni corrected p values) and was driven by a greater proportion in calcareous grassland compared to acid grassland ($z = 3.46$, $p<0.001$) and a greater proportion in heath compared to acid grassland and calcareous grassland ($z = 8.75$, $p <0.001$; $z = 5.40$, $p < 0.001$ respectively) (Fig. 5). The proportion of ground hunters was also significantly different among habitats ($X^2_{(2, N = 27)} = 23.89$, $p < 0.014$) with a greater proportion in acid grassland and calcareous grassland compared to heath ($z = 4.58$, $p <0.001$; $z = 3.86$, $p < 0.001$ respectively) (Fig. 5). The proportion of orb web weavers was not significantly different among habitats ($X^2_{(2, N = 27)} = 3.38$, $p = 0.18$) (Fig. 3).

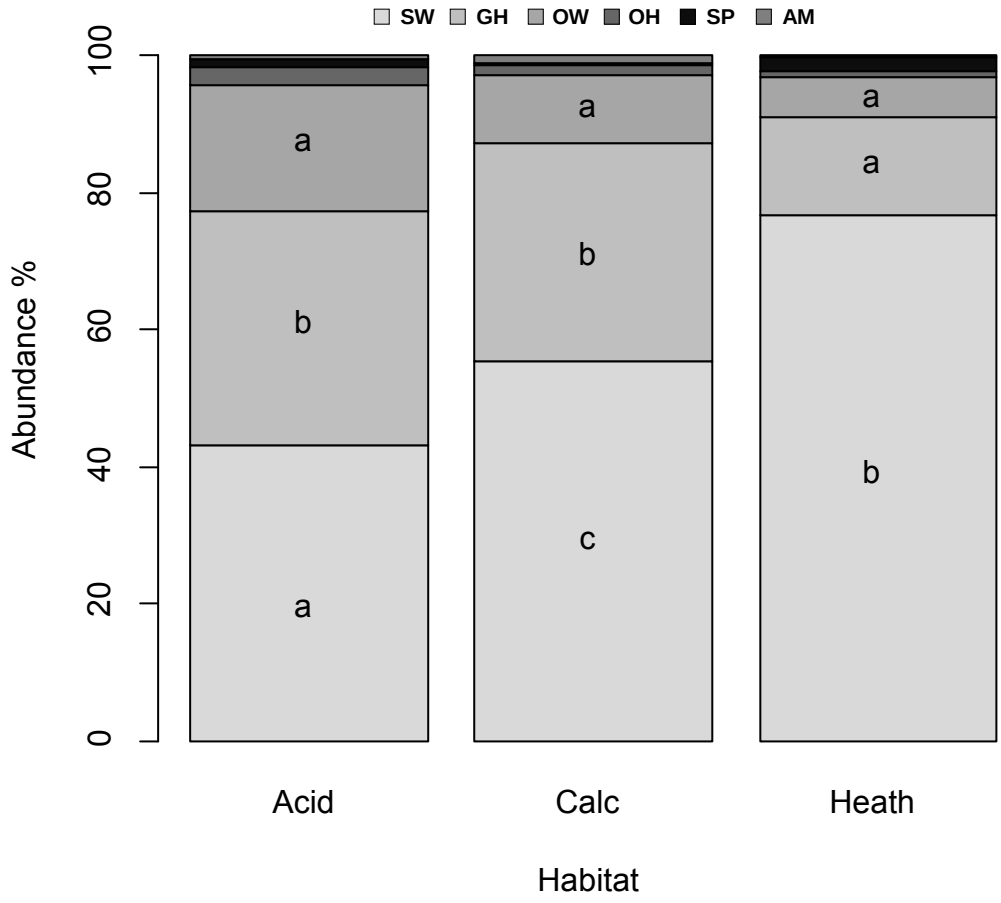

Figure 5 The proportion that each spider hunting guild makes up in each habitat type. The letters indicate significance of post hoc Tukey test within each guild; where letters are different this indicates a significant difference ($p < 0.05$) in a guild's proportional abundance among the habitat types. SW = sheet web weavers, GH = ground hunters, OW = orb web weavers, OH = 'other' hunter, SP = space web weavers, AM = ambush hunters.

Do non-target habitats support species of conservation interest?

Indicator species analysis revealed a total of three species associated with acid grassland, four with calcareous grassland and eight associated with heath (Table 1). All three species associated with acid grassland were from the sheet web weaver guild, two of which have a preference for damp habitat conditions. Three of the four species associated with calcareous grassland were from the sheet web guild, including *Jacksonella falconeri* (Jackson, 1908) which is classified as endangered by Dawson *et al.* (2008). All three species have preferences for grassland habitats. The fourth species associated with calcareous grassland belongs to the ground hunter guild and is a generalist species. Of the eight species associated with heath, six were from the sheet web guild, including *Agyneta subtilis* (O.P. Cambridge, 1863) which is classified as vulnerable by Dawson *et al.* (2008). The further two associated species were from the ground hunter and space web weaver guilds. With the exception of *Walckenaeria acuminata* Blackwall, 1833, all species associated with heath have a preference for woodland or heathland (Table 1).

Assessment of conservation status according to Dawson *et al.* (2008) revealed two endangered species: *J. falconeri* (17 individuals) and *Porrhomma egeria* Simon, 1884 (2 individuals), and six vulnerable species; *A. subtilis* (274 individuals); *Walckenaeria dysderoides* (Wider, 1834) (4 individuals); *Allomengea scopigera* (Grube, 1859) (3 individuals); *Trichopternoides thorelli* (Westring, 1861) (2 individuals); *Walckenaeria inscisa* (O.P. Cambridge, 1871) (1 individual) and *Walckenaeria monoceros* (Wider, 1834) (1 individual) (Table 2).

Table 1 Spider species associated with habitat type. Indicator Species Analysis produces an Indicator Value between 0 – 1, with values closest to 1 signifying a perfect indictor (always present in a particular treatment and exclusive to that treatment). Hunting guilds were gathered from Cardoso *et al.* (2011). Conservation status was gathered from Dawson *et al.* (2008) and habitat associations from Harvey *et al.* (2002). GH = ground hunter; SW = sheet web weaver; SP = space web weaver. $p < 0.05$ = *; $p < 0.01$ = **; $p < 0.001$ = ***.

Species	Family	Conservation Status	Hunting Guild	Habitat Association	Habitat Preference	Indicator Value
Walckenaeria vigilax	Linyphiidae	LC	SW	Acid grassland	Moss and grass in wet areas	0.616 **
Micrargus herbigradus	Linyphiidae	LC	SW	Acid grassland	Moss, leaf litter, detritus in grassland / woodland / heathland.	0.552 *
Walckenaeria antica	Linyphiidae	LC	SW	Acid grassland	Dry woodland litter or moist litter where *W. alticeps* is absent. Aeronaut.	0.513 *
Hahnia nava	Hahniidae	LC	SW	Calcareous grassland	Moss and other low vegetation and amongst stones	0.711 ***
Tiso vagans	Linyphiidae	LC	SW	Calcareous grassland	Moss, grass grasslands,	0.683 **

					wet moorland, heather. Aeronaut.	
Jacksonella falconeri	Linyphiidae	EN	SW	Calcareous grassland	Calcareous grassland, open stony areas of heathland. Uncommon. In decline.	0.510 *
Trochosa terricola	Lycosidae	LC	GH	Calcareous grassland	Wide range of habitats including: grassland / woodland / heath.	0.503 *
Tenuiphantes zimmermani	Linyphiidae	LC	SW	Heath	Woodland / heath.	0.849 ***
Ceratinella brevipes	Linyphiidae	LC	SW	Heath	Variety: Woodland / mature heathland.	0.670 **
Peponocranium ludicrum	Linyphiidae	LC	SW	Heath	Mature heathland / unimproved grassland.	0.666 ***
Pardosa nigriceps	Lycosidae	LC	GH	Heath	Heathlands / woodlands / grasslands. Partly arboreal.	0.647 **

Agyneta subtilis	Linyphiidae	VU	SW	Heath	Woodland / mature dry heath.	0.629 **
Walckenaeria acuminata	Linyphiidae	LC	SW	Heath	Ground zone of almost any habitat.	0.610 **
Pelecopsis mengei	Linyphiidae	LC	SW	Heath	Ericaceous shrubs.	0.571 *
Robertus lividus	Linyphiidae	LC	SP	Heath	Woodland / high moorland.	0.523 *

Table 2 Spiders of conservation importance with abundance in each habitat type. Hunting guilds were gathered from Cardoso *et al.* (2011). Conservation status was gathered from Dawson *et al.* (2008) and habitat associations from Harvey *et al.* (2002).

Species	Guild	Family	Conservation Status	Habitat Preferences	Acid Grassland	Calcareous Grassland	Heath
Jacksonella falconeri	SW	Linyphiidae	EN	Calcareous grassland, open stony areas of heathland. Uncommon. In decline.	2	13	2
Porrhomma egeria	SW	Linyphiidae	EN	Cavernicolous. Ecology relatively unknown.	0	0	2
Agyneta subtilis	SW	Linyphiidae	VU	Woodland / mature dry heath.	19	91	164
Allomengea scopigera	SW	Linyphiidae	VU	Wet grasslands and dry heathland.	0	0	3
Trichopternoides thorelli	SW	Linyphiidae	VU	Ground level, moss and grass. Damp areas.	2	0	0
Walckenaeria dysderoides	SW	Linyphiidae	VU	Heathland, open stony areas. Also on	0	2	2

				calcareous grassland.			
Walckenaeria incisa	SW	Linyphiidae	VU	Calcareous grassland, heathland.	0	1	0
Walckenaeria monoceros	SW	Linyphiidae	VU	Pioneer of burned heathland. Also under stones in open habitats.	0	1	0

Discussion

How do spider assemblages differ among habitats in the calcareous grassland matrix?

This study found distinct spider species assemblages between heath and both grassland habitat types, the latter not differing from each other. Additionally, despite there being no difference in species richness, β diversity was greater in both grassland habitat types compared to heath, though again the former did not differ from each other. This indicates that spider species assemblage is driven by turnover of species (both losses and gains) and is not simply a product of recruitment of species, as was also recognised by Dennis *et al.* (2015) and van Klink *et al.* (2013) in grasslands under varying management intensities.

Indeed, the differences in species assemblage are likely a result of contrasting habitat structure, which is known to impact spiders (Chapter 3, this thesis; Bell *et al.* 2001; Morris, 2000; Uetz, 1991). There is considerable variation in the structure of grasslands and heathlands (Garcia *et al.* 2010). In the present study, though heath had greater overall vegetation height than the grassland habitats, the ground layer was denser in the latter resulting in greater structural complexity at the ground level in grasslands (personal observation). Indeed, increased structural complexity provides increased potential for niche differentiation (Woodcock *et al.* 2009). In structurally complex swards containing a full range of phenological structures there is increased potential for resource utilisation for phytophagous prey taxa (Denno 1980; Woodcock *et al.* 2009; Morris, 2000), and greater abundance than in structurally less complex swards (Dennis *et al.* 1998, 2008). Further, as structural complexity increases, the availability of niches suitable for the construction of different types of webs also increases (Bell *et al.* 2011; Robinson, 1981; Woodcock *et al.* 2009).

How does functional diversity, measured by hunting strategy, differ among habitat types in the matrix?

Overall, differences of the proportions of hunting guilds among habitat types likely reflect habitat structural differences. The dominance of sheet web weavers in heath and the significantly reduced proportion of ground hunters compared to the grassland habitats reflects differences in ground level vegetation structure, differences in microclimate and shade. Differences of shade among heath and grasslands habitats is highlighted by the much lower abundance of *Xysticus cristatus* (Clerck, 1757), a shade intolerant ambush hunter which is rare in woodlands and closed canopy habitats (Spider and Harvestman Recording Scheme, 2017). This is further reflected by all but one of the species associated with heath having a habitat preference for woodland or heathland, six of which occupy the ground zone, often casting webs close to the ground e.g. *Peponocranium ludicrum* (O.P. Cambridge, 1861) (Harvey *et al.* 2002). The single heath associated species without a particular preference for woodland or heathland, *Walckenareia acuminata* Blackwall, 1833, is a habitat generalist, but again occupies the ground zone (Harvey at al. 2002).

The greater proportion of ground hunters in grassland habitats reflects the crucial role of refuges within the sward, such as those of tussock forming grasses, in habitat suitability for ground dwelling predators (Woodcock *et al.* 2009; Malfait and De Keer, 1990). For example, *Trochosa terricola*, associated with calcareous grassland in the present study, utilises tufts of *Festuca ovina* (Workman, 1978), the second most abundant plant species in these upland calcareous grasslands (Chapter 2, this thesis). Further, in both grassland habitats the ground hunter guild was dominated by *Pardosa* species, a genus known to also utilise different components of vegetation structure for prey capture, overwintering and refuge from predators (Bristowe, 1958; Maelfait and De Keer, 1990). In contrast, the

ground layer of the heather lacked the structural heterogeneity of the grassland habitats and is reflected by the lower proportion of ground hunters. Indeed, *Pardosa nigriceps*, the ground hunter associated in this study with heath, is a semi arboreal species (Vlijm and Kessler-Geschiere, 1967) able to utilise the contrasting structural complexity of the mature heather and as such is not as reliant on ground vegetation heterogeneity as other species in the *Pardosa* genus.

The reduced proportion of sheet web weavers in acid grassland compared to calcareous grassland was seemingly replaced by an increase in the proportion of orb web weavers, which consisted of a single species (*P. degeeri*). McFerran *et al.* (1994) and Maelfait and De Keer (1990) found *P. degeeri* was an indicator species of less intensively managed sites. Their association with acid grassland in the current study may reflect the lower effective stocking density in this habitat type, which is a product of sheep grazing behaviour. Sheep are preferential grazers, able to select preferred plant species within a sward (Grant *et al.* 1985). Where preferred vegetation is available sheep avoid *Nardus stricta* (Grant *et al.* 1985), the dominant species in the acid grassland habitat. This likely results in a lower effective stocking density in the acid grassland habitat compared to the calcareous grassland, thus providing suitable conditions for *P. degeeri*.

Do non-target habitats support species of conservation interest?

Both calcareous grassland and the non-target habitats of acid grassland and heath supported several notable species. *J. falconeri*, found in each habitat type but most abundantly in calcareous grassland, is classed as endangered in Britain (Dawson *et al.* 2008) (Table 2), and has shown a steep decline over the last 20 years (Spider and Harvestman Recording Scheme, 2017). Threats to this species include degradation and loss

of calcareous grassland and heathland (Spider and Harvestman Recording Scheme, 2017). The close proximity of these two habitat types in the present study may be beneficial for its long-term conservation.

In addition to *J. falconeri*, calcareous grassland supported four species classed by Dawson *et al.* (2008) as vulnerable in Britain: *A. subtilis, W. dysderoides, W. incisa* and *W. monoceros*, the latter two represented exclusively in this habitat by single individuals (Table 2). *W. monoceros*, which occurs under stones in open inland habitats (Harvey *et al.* 2002) and is also identified as a pioneer species of heather (Merrett, 1976), has also previously been recorded in calcareous grassland (Spider and Harvestman Recording Scheme, 2017). It has experienced steep decline in Britain over the last 20 years, with the loss of heathland and the lack of its management to maintain early successional stages implicated in this decline (Spider and Harvestman Recording Scheme, 2017). *W. dysderoides*, which was found in calcareous grassland and the non-target habitat of heath in the present study, is an uncommon species found on heathland in Southern England, woodlands and acid and calcareous grassland (Harvey *et al.* 2002). The loss of calcareous grassland and heath have been recognised as potential causes of its long-term decline, though understanding of its ecology remains relatively unknown, rendering it difficult to appreciate the mechanisms of its decline (Spider and Harvestman Recording Scheme, 2017).

There were a further two vulnerable species recorded in the non-target habitat of acid grassland (Table 2): *A. subtilis* and *T. thorelli*, the latter represented exclusively in this habitat by two individuals.

In heath two individuals of *P. egeria*, classed as endangered in Britain (Dawson *et al.* 2008), were recorded (Table 2). *P. egeria* is predominantly a cavernicolous species which usually occurs in low numbers (Harvey *et al.* 2002) and is noted as having suffered decline of 70% (Spider and Harvestman Recording Scheme, 2017). Though the phenology and ecology of this species is relatively unknown its presence within patches of heath not targeted by conservation management in this study highlight the importance of this habitat type within the calcareous grassland matrix beyond providing a distinct spider assemblage.

In addition to the endangered species mentioned, heath also supported three species classed by Dawson *et al.* (2008) as vulnerable (Table 2); *A. scopigera* which was again exclusive to this habitat, *W. dysderoides* and *A. subtilis*, the latter of which occurs in greater abundance in this habitat (164 individuals) compared to each of the grassland habitat types (acid grassland = 19 individuals; calcareous grassland = 91 individuals). *A. subtilis* has been noted as maintaining high densities in mature heather of dry heath after burning (Merrett, 1990). Its comparatively high abundance in heath in the present study again highlight the importance of this habitat type in the calcareous grassland matrix.

Conservation Implications

The absence of targeted management of heath patches within the upland calcareous grassland matrix, coupled with the low stocking density of sheep, results in them being relatively undisturbed. Consequently, they support a distinct spider assemblage and a number of notable species. It is recommended that the introduction of management for some of these non-target habitat patches to promote early successional stages of heather, thus further increasing habitat heterogeneity, may be beneficial for the conservation of a number of notable spider species. However, the impact of such management on individual

species should be carefully considered prior to implementation and should be closely monitored post-management. Where *W. monoceros* has been recorded, targeting management of heather patches close to limestone scree or rubble, accounting for the spider's association with stones in open habitats, may have greater results than targeting heath patches which are not in close proximity to stones. However, before implementation of such management the presence of *P. egeria* on a site should be considered. Where this species is found to be present in a heather patch non-intervention would be recommended. It is noted, however, that outcomes of such management recommendations are hypotheses only, based on current understanding of species ecological requirements. Impacts of such alterations in management on spiders, as well as other components of biodiversity, must be closely monitored.

Conclusions

The importance of the calcareous grassland habitat mosaic has been demonstrated in this study by the distinct species assemblages between heath and the grassland habitats and by the different proportion of guilds in these assemblages.

This study highlights the value of monitoring biodiversity in non-target habitats within a habitat matrix alongside those that are actively targeted by management. Understanding which species occur within these non-target habitats and their ecology is vitally important in making management decisions. This highlights the importance of integrating research with conservation management and further research into the overall biodiversity value of these non-target habitats within the calcareous grassland matrix is urged.

Chapter 5

Conclusions

Conservation management and monitoring of calcareous grassland typically focuses on vegetation, with little attention paid to invertebrates despite their importance in ecosystem functioning (Poschlod and Wallis de Vries, 2002; Wallis de Vries *et al.* 2002). Indeed, grazing management for many open landscapes still lacks a good evidence base, particularly for insect communities (Wallis de Vries *et al.* 2016). This research is the first assessment of the responses of plants, carabid beetles and spiders in relation to commonly used grazing regimes in upland calcareous grasslands. It also provides the first assessment of the spider species supported by non-target habitats in the upland calcareous grassland matrix. In addition, this research provides evidence base management recommendations for the first time for both non-target habitats and non-target taxa.

The impacts of grazing on plants, carabid beetles and spiders in upland calcareous grasslands

This study shows that grazing intensity is the major driver of vegetation diversity and structural complexity, which indirectly affects carabid beetle and spider species assemblages, likely by altering niche availability and aspects of microclimate in addition to disturbance caused directly by livestock (Chapters 2 and 3). This is demonstrated by the similar carabid beetle and spider species assemblages revealed in this study in the light stocking intensities of cattle and sheep grazing (Chapters 2 and 3), despite having distinct plant species compositions (Chapter 2). Rather, under both grazing types the effects of livestock species on vegetation structural complexity was similar, as indicated by

comparable vegetation height (Chapter 2) and detailed measures of structural complexity (Chapter 3). This is supported by the strong associations of carabid beetle and spider species that utilise tussock forming grasses (e.g. species from *Carabus* and *Pardosa* genera) (Chapters 2 and 3) which were also associated with light cattle and light sheep grazing (Chapter 2). In contrast, the increased vegetation structural complexity in ungrazed regimes resulted in distinct carabid beetle and spider species assemblages (Chapters 2 and 3) whilst the much reduced structural complexity in heavy sheep grazing produced a distinct spider assemblage (Chapter 3). Furthermore, there were a number of notable species from both arthropod taxa associated with each grazing regime, highlighting the contribution of each to invertebrate diversity (Chapters 2, 3 and 4).

The value of non-target habitats to biodiversity

The presence of patches of acid grassland and heath not targeted by conservation management in the calcareous grassland matrix increases the heterogeneity of the landscape. The value of these non-target habitats in the calcareous grassland matrix was demonstrated by the distinct spider species assemblages found between heath and grassland habitats and by the unique species of conservation importance supported in acid grassland and heath (Chapter 4). The presence of mature heather, in an otherwise treeless landscape, provided suitable habitat conditions for several spider species usually associated with woodland. This may be important in assisting with dispersal and providing refuge for rare species in an increasingly fragmented landscape. The association of unique rare spider species in the non-target habitats of acid grassland and heath also demonstrates their value within the calcareous grassland matrix. Further, it is likely that the value of heather patches within this landscape may be improved by targeting conservation management towards some of them. The vast majority of the heather patches are in the mature stage of

the heather cycle. Targeting some of these patches to promote early successional and building stages of heather may further contribute to their biodiversity value, for example by providing conditions for vulnerable pioneer species such as *W. monoceros*. The spider associations with non-target habitats revealed by this study highlight their importance.

Management recommendations for upland calcareous grasslands and associated habitats

This study demonstrates the differing impacts of grazing regimes on plants, carabid beetles and spiders and enable the first evidence based management recommendations which incorporate multiple taxa to be made. These are outlined below:

- Promote heterogeneous vegetation structural complexity across the landscape via:
    - Cessation of high intensity grazing – high intensity sheep grazing is not uncommon in upland regions of Britain. The community of commonly found disturbance tolerant pioneer spiders associated with this grazing regime has little in common with the diverse assemblages that could be supported by lighter grazing regimes and as such it is recommended that stocking intensities of this grazing regime are reduced to less than the recommended intensity of 0.25 LU ha^{-1} yr^{-1} for maintaining biodiversity (Backshall *et al.* 2001).
    - Inclusion of both low intensity sheep grazing and low intensity cattle grazing – intermediate structural complexity produced by low intensity sheep grazing and low intensity cattle grazing regimes provides suitable habitat conditions for a number of rare carabid beetle and spider species, which were unique to each regime. Owing to the unique rare arthropod species supported by light sheep and light cattle grazing regimes, coupled with the similarity in plant species richness and overlap of plant species

compositions, the current trend to replace low intensity sheep grazing with low intensity cattle grazing is not necessary.

- Promote ungrazed compartments – ungrazed compartments are rare across the upland landscape. Their value in supporting distinct carabid beetle and spider species assemblages, and unique rare species, emphasises their importance. The introduction of additional ungrazed compartments across the landscape is encouraged. It is recommended that areas selected for cessation of grazing are targeted to provide maximum benefit to long term botanical diversity, as well as invertebrate diversity. For example, reducing grazing in areas with deposits of glacial till may encourage patches of heather regeneration, which have been demonstrated to benefit spider fauna (Chapter 3). Further, in order to avoid the loss of calcareous grassland botanical diversity, rotational cessation and reintroduction of grazing across a number of compartments is recommended. Reintroduction of grazing should take place prior to scrub encroachment and before seed bank diversity is diminished. Whilst this will differ between sites, previous research suggests seed bank species composition in ungrazed grassland is significantly different after 11 years of no grazing (Jacquemyn *et al.* 2011). With this in mind, it is recommended that grazing is reintroduced either when the first signs of scrub encroachment are observed or after a maximum of 10 years. Further, the method of reintroduction of management may assist in botanical restoration of ungrazed calcareous grasslands. Reintroduction of sheep grazing can re-establish species richness via dispersal of seeds from other calcareous grasslands (Poschlod and Bonn, 1998). It is unknown if cattle fulfil the same role and as such it is

recommended that reintroduction of grazing is with sheep that have been grazing on local calcareous grasslands. Further, maintaining a time series of ungrazed compartments may also provide intermediate successional stages of habitat suitable for other taxa, though this requires further investigation.

- Active management of non-target habitats:
    - Development of heath patches - The non-target habitats of acid grassland and heath provide suitable conditions for rare spider species, and in the case of heath, support a distinct spider species assemblage. The development of heath patches is recommended and could be achieved by the cessation of grazing across whole compartments or through the exclosure of livestock on deposits of glacial till that have the potential to develop into heath. The size of these areas will vary depending on the deposits of glacial till. However, it is recommended that such heather development is focused on deposits at least $20m^2$, comparable to those for which there is now an evidence base from results of this study.
    - Maintain established heath patches – to maintain suitable habitat for distinct spider communities, heath patches should be maintained by the use of low intensity grazing. The presence of heath patches in compartments of low intensity sheep grazing render this an appropriate grazing regime and its continuation is recommended.
    - Promote a range of successional stages among heath patches – introduction of management to some patches of heath would further increase habitat heterogeneity in the upland calcareous grassland matrix. This may be achieved by cutting, in which case care must be taken to remove resultant litter to ensure germination of seedlings is not inhibited. It may also be

achieved by controlled burning, however caution must be taken with this method to prevent the spread of fire and must only be performed during the wetter winter months. Regardless of the method of management, heath patches subjected to management should be targeted to encourage positive conservation outcomes e.g. target patches close to limestone outcrops or rubble to provide a transition for species such as *W. monoceros* which is found under stones and as a pioneer of burned heath. Equally, avoiding management in heath patches where species such as *P. egeria*, a cavernicolous species which may rely on the shade of mature heather, are present.

Landscape scale management

To maintain heterogeneous structural complexity across the landscape using a range of management regimes, cooperation of a number of conservation organisations, private land owners and graziers is vitally important in order to coordinate management efforts. The suitability of individual compartments to a particular management type will be influenced by environmental conditions, logistics and economics.

It is recognised that changes in management may result in loss of income via loss of subsidies or due to loss of stock available for sale. Where cessation of grazing is recommended it is advised that as a minimum any subsidy payments are maintained and that further compensation to account for the loss of income from reducing stock is provided. This may require a change to options in Countryside Stewardship agreements and requires consultation and cooperation with Natural England.

Future Research in Upland Calcareous Grasslands

This study examined the impacts of commonly used grazing regimes that had been in place for a minimum of ten years, on plants, carabid beetles and spiders in upland calcareous grasslands. It did not attempt to quantify the impact of grazing duration or timing, which is known to impact some taxa in other grassland systems (e.g. birds (Tichit *et al.* 2005); small mammals (Schmidt *et al.* 2005); plants (Smith *et al.* 2000); butterflies (Van Noordwijk *et al.* 2012)), on any of the studied taxa. Such studies would contribute to the further understanding of grazing impacts. However, due to the rarity of calcareous grasslands, replication of a chronosequence study is not possible. Thus, studies on experimentally controlled grazing regimes could provide valuable information which may be beneficial for the long term conservation of these internationally important habitats. In addition, it is also noted that the time taken for each of the studied taxa to reach equilibrium after changes in management is also unknown. For this reason, it is recommended that any experimental alteration of management should be monitored as part of a long term (minimum 10 years) study in order to quantify the point of equilibrium and to ensure management recommendations from such experimental studies are applicable to long term management regimes.

Additionally, though this study recommends maintaining ungrazed areas, pressure to conserve the characteristic vegetation of upland calcareous grassland is driving a move to reintroduce grazing in ungrazed calcareous grasslands among conservation organisations. Any such changes in management would present further opportunities to gain an understanding into the responses of arthropods and plants to these management changes and it is urged that baseline surveys, prior to the reintroduction of grazing, along with surveys after reintroduction of grazing are conducted. Monitoring plant species turnover

after the reintroduction of grazing with both cattle and sheep from local calcareous grasslands would determine the most beneficial livestock type for the reintroduction of management to ungrazed calcareous grasslands for plant diversity. Where cessation of grazing is introduced, annual monitoring of vegetation composition and seed bank composition is recommended in addition to measures of vegetation structural complexity and a range of invertebrate functional groups e.g. phytophageous, detritivore and predatory taxa.

Furthermore, upland calcareous grassland landscapes consists of a heterogeneous patchwork of habitats within a matrix including calcareous grassland, acid grassland, heath, and limestone pavement. Due to the challenges of sampling and time constraints, the latter was beyond the scope of this study. However, given the relict woodland floor community in the grikes of limestone pavement coupled with the potential for contrasting microclimates impacted by vegetation cover and shade, investigations into invertebrate communities associated with the grikes of limestone pavement may provide further insight into the dispersal of invertebrate species across the landscape, informing management.

Until now the value of non-target habitats to biodiversity in the upland calcareous grassland matrix was unknown. The assessment of the epigeal spider fauna supported by these non-target habitats in this study is the first quantification of their biodiversity value. Though this study provided insights into the value of non-target habitats to spiders, their value to other invertebrate taxa remains unknown. It is therefore strongly urged that prior to introduction of active management, surveys of other taxa, such as a invertebrates from a variety of functional groups e.g. phytophageous, predatory and detritivore taxa, are completed so that management can be targeted in the most appropriate way for a range of

taxa. Further, the homogeneity of heather growth stage currently present offers a unique opportunity to investigate aspects which may influence both individual species and assemblages, such as proximity to limestone outcrops, patch size and isolation from other patches, which will be lost at the introduction of management. It is therefore recommended that prior to the introduction of management such measurements are collected for analysis along with surveys of other taxa. Additionally, heath habitat patch size is largely dependent on underlying deposits of glacial till. The effect of heath patch size in the calcareous grassland matrix on invertebrates is unknown. Investigation into invertebrate assemblages in heath patches of differing sizes will also aid in targeting areas for promoting heath development.

The introduction of active management to produce a range of successional stages of heather must also be accompanied by research which monitors the impact of such changes in management on spiders and other invertebrate taxa. The importance of monitoring changes in management on a range of taxa is stressed. Monitoring a range of taxa will ensure the detection of early warning signs of detrimental practices, or indeed positive impacts on biodiversity, and will enable dynamic conservation management to provide the best possible outcomes for biodiversity at large.

Concluding remarks

This study shows that in addition to supporting a rich and diverse flora, upland calcareous grasslands also support rich and diverse assemblages of carabid beetles and spiders, including several rare species. This study contributes to the mounting evidence that the response of arthropod diversity to grazing deviates from that of plants (e.g. Kruess and Tscharntke, 2002; Pöyry *et al.* 2006; Zhu *et al.* 2012).

The findings of this study and the management recommendations arising from it are applicable beyond the upland calcareous grasslands of Britain. Comparable habitats with similar conservation issues exist in other parts of Europe (e.g. the Burren, Ireland; Franconian Jura, Germany; Stora Alvaret, Sweden). Conservation of calcareous grasslands across Europe could be enhanced through international collaboration of researchers and conservation practitioners.

In addition, the approach of considering biodiversity within the upland calcareous grassland matrix in this study is novel. Though heath is often a conservation priority in other landscapes with management geared towards its maintenance or restoration, it is generally the sole management target and is not considered as part of a matrix. Incorporating it into upland calcareous areas, as in this study, is novel and could greatly enhance knowledge on its contribution to overall biodiversity. In contrast acid grassland is rarely a conservation priority, unless it houses a specific rare species (e.g. Marsh Fritillary) on wet grassland. Again recognising its value as part of a matrix is a novel approach. This matrix approach to monitoring and conserving biodiversity is important and is demonstrated in this study.

In addition to the recommendation of monitoring invertebrate responses to different grazing regimes, targeting management to promote heterogeneous invertebrate assemblages across the landscape is urged. This can only be achieved by integrating research and conservation management.

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Appendices

A1. Species of vascular plant, bryophyte and carabid beetles recorded. For vascular plants and bryophytes total per cent cover for each grazing regime is the sum of the mean covers for each site across each grazing regime. For carabid beetles, abundance for each grazing regime is the sum of all sites.

Vascular Plant Species	Ungrazed	Cattle	Sheep		Carabid Beetle Species	Ungrazed	Cattle	Sheep
	Total % Cover					Abundance		
Achillea millefolium	1.00	2.83	6.50		*Abax parallelpipedus*	85	306	46
Agrostis capillaris	13.17	18.67	8.00		*Amara lunicollis*	6	3	0
Agrostis stolonifera	41.33	22.50	26.17		*Badister bullatus*	2	0	1
Alchemilla spp	1.50	0.00	0.00		*Calathus fuscipes*	0	22	28
Anacamptis pyramidalis	0.00	0.50	1.33		*Calathus melanocephalus*	0	0	1
Anemone nemorosa	0.00	0.00	0.50		*Carabus arvensis*	1	29	8
Anthoxanthum odoratum	45.00	72.33	155.17		*Carabus nemoralis*	0	1	1
Avenula pratensis	3.00	2.33	10.83		*Carabus problematicus*	4	3	8
Bellis perennis	0.00	0.50	0.00		*Carabus violaceus*	4	36	60
Betonica officinalis	6.00	0.00	0.00		*Clivina fossor*	10	9	4
Betula spp	1.00	0.00	0.00		*Cychrus caraboides*	23	30	19
Botrychium lunaria	0.00	0.00	0.50		*Harpalus latus*	10	26	21
Brachypodium sylvaticum	0.50	0.00	0.00		*Leistus terminatus*	7	3	3
Briza media	9.17	23.17	25.50		*Loricera pilicornis*	0	0	1
Calluna vulgaris	0.00	1.00	2.33		*Notiophilus germinyi*	4	3	56
Campanula rotundifolia	11.00	9.50	6.50		*Pterostichus aethiops*	1	10	7
Cardamine pratensis	0.00	0.00	1.00		*Pterostichus cristatus*	0	0	1
Carex demissa	0.00	0.50	0.00		*Pterostichus madidus*	768	1734	1561
Carex flacca	85.00	200.50	113.67		*Pterostichus melanarius*	23	246	352
Carex panicea	0.50	8.17	3.00		*Stomis pumicatus*	11	1	7
Carex pulicaris	1.00	1.50	1.00		*Synchus vivalis*	0	4	19
Cerastium fontanum	1.00	1.50	6.00		*Trechus obtusus*	104	11	28
Conopodium majus	0.00	0.00	0.50		*Trechus secalis*	1	64	27
Cynosurus cristatus	0.00	1.33	3.83					
Dactylis glomerata	5.17	0.00	0.00					
Danthonia decumbens	0.00	5.00	3.50					
Deschampsia cespitosa subsp. cespitosa	13.33	1.00	4.67					
Deschampsia flexuosa	0.00	0.00	0.50					
Empetrum nigrum subsp. nigrum	1.00	0.00	0.00					
Epilobium brunnescens	0.00	0.50	0.00					
Erica cinerea	0.00	0.00	1.00					

Euphrasia ssp	3.50	3.50	6.00					
Festuca ovina	278.17	300.67	197.67					
Festuca rubra	0.00	0.00	1.33					
Filipendula ulmaria	0.50	0.00	0.00					
Filipendula vulgaris	0.00	0.00	2.50					
Fragaria vesca	0.50	0.50	1.50					
Galium saxatile	5.00	2.50	2.00					
Galium sterneri	9.50	13.00	16.00					
Galium verum	8.50	5.33	13.33					
Gentianella amarella	0.00	0.50	0.00					
Gymnadenia conopsea	0.50	0.00	0.00					
Helianthemum nummularium	27.00	2.00	4.00					
Hieracium spp	1.00	0.00	0.00					
Holcus lanatus	1.33	2.00	2.50					
Koeleria macrantha	23.50	30.67	27.33					
Lathyrus tuberosus	0.00	0.00	5.83					
Linum catharticum	2.50	11.50	8.50					
Lotus corniculatus	6.50	17.00	17.17					
Luzula campestris	1.50	3.50	5.00					
Nardus stricta	0.50	2.50	1.50					
Neottia ovata	1.00	0.00	1.00					
Orchis mascula	2.00	0.00	0.00					
Pilosella officinarum	0.50	6.17	8.00					
Plantago lanceolata	0.00	5.00	6.50					
Plantago media	0.00	5.00	6.33					
Poa trivialis	0.00	1.50	0.50					
Potentilla erecta	22.17	36.17	24.67					
Potentilla sterilis	2.00	1.50	2.50					
Poterium sanguisorba ssp sanguisorba	14.83	6.33	11.83					
Primula farinosa	0.00	0.50	2.00					
Prunella vulgaris	0.00	4.00	3.00					
Ranunculus acris	0.50	7.00	6.00					
Ranunculus bulbosus	1.50	5.00	8.50					
Sanguisorba officinalis	3.33	0.50	2.50					
Scabiosa columbaria	0.00	0.00	0.50					
Senecio jacobaea	1.50	1.50	0.00					
Sesleria caerulea	607.83	509.50	602.83					
Succisa pratensis	5.00	0.50	0.00					
Taraxacum officinale agg.	0.00	1.00	1.50					
Thymus polytrichus	13.67	35.50	21.33					
Trifolium repens	4.00	19.33	22.67					
Vaccinium myrtillus	2.00	4.50	0.00					
Veronica chamaedrys	1.50	1.00	3.00					

Veronica officinalis	0.00	3.00	2.50					
Vicia cracca	0.00	0.50	1.83					
Viola hirta	2.00	0.00	0.00					
Viola riviniana	20.50	29.67	26.33					
Viola tricolor	0.00	0.00	0.50					
Bryophyte Species	Ungrazed	Cattle	Sheep					
Calliergonella cuspidata	0.00	0.00	1.00					
Calliergonella cuspidata	1.00	0.00	0.00					
Dicranum scoparium	7.00	24.17	4.50					
Hylocomium splendens	42.17	49.00	23.50					
Hypnum jutlandium	0.00	1.50	0.00					
Jungermannia atrovirens	0.00	0.50	0.00					
Morpho speceis 5	0.00	1.00	0.00					
Morpho species 1	1.00	2.50	0.00					
Morpho species 2	1.00	0.00	0.00					
Morpho species 3	0.50	1.00	0.50					
Morpho species 4	0.50	3.67	1.00					
Morpho species 6	1.00	1.00	0.00					
Morpho species 7	0.00	0.00	0.50					
Necora crispa	0.50	1.00	0.50					
Plagiomnium undulatum	0.00	0.00	0.50					
Pleurozium schreberi	0.00	1.00	0.00					
Polytrichastrum formosum	0.00	0.50	0.00					
Polytrichum spp	0.50	0.00	0.00					
Pseudoscleropodium purum	25.50	57.50	29.17					
Pyridium molluscum	9.50	7.83	2.50					
Racomitrium lanuginosum	2.50	12.17	7.17					
Rhytidiadelphus squarrosus	14.33	21.33	21.83					
Tortella tortuosa	0.50	0.00	0.00					

A2: Spider species abundance for each grazing regime calculated as the sum of all sites after standardisation by trap day. Hunting guilds based on Cardoso *et al.* (2011) and conservation status from Dawson *et al.* (2008). Nomenclature follows World Spider Catalogue (2017). SW = sheet web weavers, GH = ground hunters, OW = orb web weavers, OH = 'other' hunter, SP = space web weavers, AM = ambush hunters, EN = endangered, VU = vulnerable, LC = least concern.

Species	Guild	Family	Conservation Status	Ungrazed	Cattle	Light Sheep	Heavy Sheep
Agroeca proxima	GH	Liocranidae	LC	11	1	14	0
Agyneta cauta	SW	Linyphiidae	LC	6	2	43	1
Agyneta conigera	SW	Linyphiidae	LC	12	6	26	1
Agyneta decora	SW	Linyphiidae	LC	5	33	11	17
Agyneta olivacea	SW	Linyphiidae	LC	1	5	2	0
Agyneta ramosa	SW	Linyphiidae	LC	0	1	0	0
Agyneta subtilis	SW	Linyphiidae	VU	138	32	91	3
Allomengea scopigera	SW	Linyphiidae	VU	0	7	0	0
Alopecosa pulverulenta	GH	Lycosidae	LC	47	62	28	38
Antistea elegans	SW	Hahniidae	LC	1	0	0	0
Asthenargus paganus	SW	Linyphiidae	LC	1	0	0	0
Bathyphantes gracilis	SW	Linyphiidae	LC	0	4	2	20
Bathyphantes parvulus	SW	Linyphiidae	LC	25	2	3	0
Bolyphantes luteolus	SW	Linyphiidae	LC	0	2	3	2
Centromerita bicolor	SW	Linyphiidae	LC	0	0	0	1
Centromerita concinna	SW	Linyphiidae	LC	1	6	19	5
Centromerus dilutus	SW	Linyphiidae	LC	8	0	3	0
Centromerus prudens	SW	Linyphiidae	LC	0	3	5	1

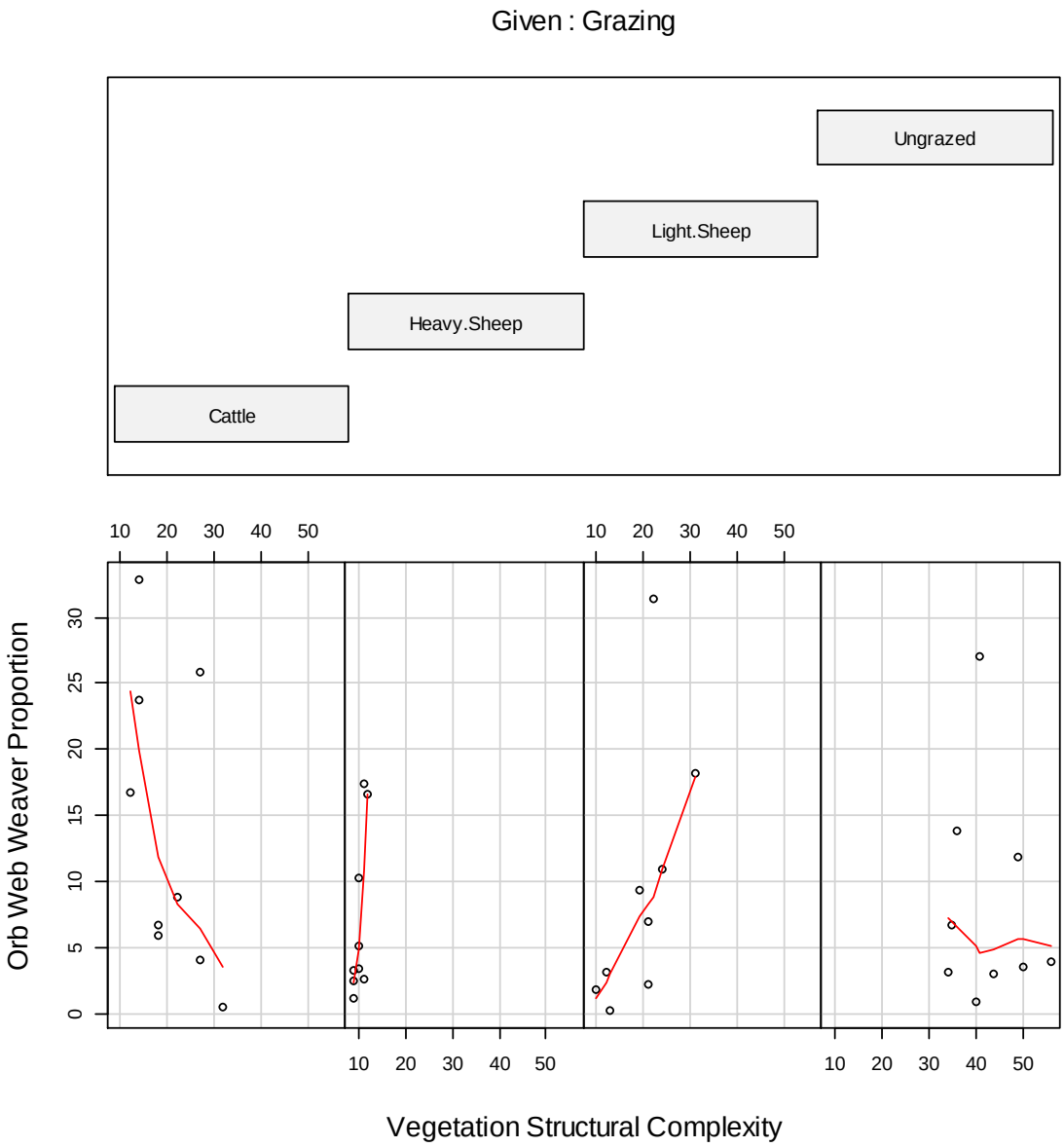
Ceratinella brevipes	SW	Linyphiidae	LC	5	8	8	4
Ceratinella brevis	SW	Linyphiidae	LC	4	1	1	0
Clubiona diversa	O	Clubionidae	LC	3	0	6	2
Clubiona reclusa	O	Clubionidae	LC	1	0	0	0
Cnephalocotes obscurus	SW	Linyphiidae	LC	1	1	0	0
Coelotes atropos	SW	Agelenidae	LC	1	9	19	0
Dicymbium tibiale	SW	Linyphiidae	LC	1	49	21	177
Diplocephalus latifrons	SW	Linyphiidae	LC	0	0	1	0
Dismodicus bifrons	SW	Linyphiidae	LC	3	2	0	0
Drassodes cupreus	GH	Gnaphosidae	LC	1	10	4	3
Drassyllus pusillus	GH	Gnaphosidae	LC	0	3	1	0
Erigone atra	O	Linyphiidae	LC	0	0	1	135
Erigone dentipalpis	O	Linyphiidae	LC	0	0	3	149
Erigonella hiemalis	O	Linyphiidae	LC	3	4	5	1
Gonatium rubens	SW	Linyphiidae	LC	13	7	8	0
Gongylidiellum vivum	SW	Linyphiidae	LC	11	38	0	17
Hahnia montana	SW	Hahniidae	LC	9	0	6	3
Hahnia nava	SW	Hahniidae	LC	1	5	22	3
Haplodrassus signifer	GH	Gnaphosidae	LC	3	8	8	0
Hypomma bituberculatum	SW	Linyphiidae	LC	0	2	4	0
Jacksonella falconeri	SW	Linyphiidae	EN	5	14	13	18
Lophomma punctatum	SW	Linyphiidae	LC	0	0	0	1
Maro minutus	SW	Linyphiidae	VU	0	1	0	0
Meioneta beata	SW	Linyphiidae	LC	2	6	13	2
Meioneta saxatilis	SW	Linyphiidae	LC	1	2	0	1
Micaria pulicaria	GH	Gnaphosidae	LC	0	2	0	0
Micrargus apertus	SW	Linyphiidae	LC	3	0	0	0

Micrargus herbigradus	SW	Linyphiidae	LC	18	37	24	20
Micrargus subaequalis	SW	Linyphiidae	LC	0	0	3	0
Microlinyphia pusilla	SW	Linyphiidae	LC	1	0	0	0
Monocephalus fuscipes	SW	Linyphiidae	LC	77	8	29	9
Neon reticulatus	O	Salticidae	LC	7	0	0	0
Oedothorax apicatus	O	Linyphiidae	LC	0	0	1	1
Oedothorax fuscus	O	Linyphiidae	LC	0	0	1	283
Oedothorax gibbosus	O	Linyphiidae	LC	0	8	2	55
Oedothorax retusus	O	Linyphiidae	LC	5	119	32	426
Oedothorax agrestis	O	Linyphiidae	LC	0	0	0	5
Ostearius melanopygius	SW	Linyphiidae	LC	0	0	0	1
Ozyptila antomaria	AM	Thomisidae	LC	2	1	3	2
Ozyptila trux	AM	Thomisidae	LC	9	0	2	0
Pachygnatha degeeri	OW	Tetragnathidae	LC	239	562	324	167
Palliduphantes ericaeus	SW	Linyphiidae	LC	438	215	190	36
Palliduphantes insignis	SW	Linyphiidae	LC	0	0	1	2
Palliduphantes pallidus	SW	Linyphiidae	LC	21	0	0	0
Pardosa nigriceps	GH	Lycosidae	LC	56	64	22	2
Pardosa palustris	GH	Lycosidae	LC	0	41	45	31
Pardosa prativaga	GH	Lycosidae	LC	2	6	1	0
Pardosa pullata	GH	Lycosidae	LC	555	1153	774	155
Pardosa agricola	GH	Lycosidae	LC	0	6	0	0
Pelecopsis mengei	SW	Linyphiidae	LC	1	0	1	0
Pelecopsis parallela	SW	Linyphiidae	LC	0	0	0	1
Peponocranium ludicrum	SW	Linyphiidae	LC	2	5	14	3
Pholcomma gibbum	SW	Linyphiidae	LC	2	0	1	0
Pirata hygrophilus	GH	Lycosidae	LC	1	0	0	1

Pocadicnemis pumila	SW	Linyphiidae	LC	466	143	264	11
Poeciloneta variegata	SW	Linyphiidae	LC	0	0	1	0
Porrhomma egeria	SW	Linyphiidae	EN	1	0	0	0
Porrhomma montanum	SW	Linyphiidae	LC	0	0	0	1
Robertus lividus	SP	Theridiidae	LC	42	8	11	2
Saaristoa abnormis	SW	Linyphiidae	LC	36	5	26	4
Savignia frontata	SW	Linyphiidae	LC	0	2	3	4
Semljicola faustus	SW	Linyphiidae	LC	0	14	0	1
Silometopus elegans	SW	Linyphiidae	LC	102	455	441	190
Tapinocyba praecox	SW	Linyphiidae	LC	2	1	9	2
Tenuiphantes cristatus	SW	Linyphiidae	LC	0	0	1	0
Tenuiphantes mengei	SW	Linyphiidae	LC	158	189	209	24
Tenuiphantes tenebricola	SW	Linyphiidae	LC	0	0	2	1
Tenuiphantes tenuis	SW	Linyphiidae	LC	0	6	6	13
Tenuiphantes zimmermanni	SW	Linyphiidae	LC	5	1	4	0
Tiso vagans	SW	Linyphiidae	LC	26	175	167	282
Trichopternoides thorelli	SW	Linyphiidae	VU	0	4	0	0
Trochosa terricola	GH	Lycosidae	LC	44	131	158	83
Walckenaeria acuminata	SW	Linyphiidae	LC	24	14	13	4
Walckenaeria antica	SW	Linyphiidae	LC	50	64	73	38
Walckenaeria atrotibialis	SW	Linyphiidae	LC	17	0	0	0
Walckenaeria cuspidata	SW	Linyphiidae	LC	2	0	0	0
Walckenaeria dysderoides	SW	Linyphiidae	VU	5	5	2	1
Walckenaeria incisa	SW	Linyphiidae	VU	1	8	1	0
Walckenaeria monoceros	SW	Linyphiidae	VU	0	0	1	0
Walckenaeria nudipalpis	SW	Linyphiidae	LC	1	0	0	0
Walckenaeria obtusa	SW	Linyphiidae	VU	1	1	0	0

Walckenaeria vigilax	SW	Linyphiidae	LC	2	12	30	32
Xysticus cristatus	AM	Thomisidae	LC	0	13	29	37

A3: Coplot with each panel representing the relationship between space web weaver abundance and vegetation structural complexity for each grazing regime.



A4: Spider species abundance for each grazing regime calculated as the sum of all sites after standardisation by trap day. Hunting guilds based on Cardoso *et al.* (2011) and conservation status from Dawson *et al.* (2008). Nomenclature follows World Spider Catalogue (2017). SW = sheet web weavers, GH = ground hunters, OW = orb web weavers, OH = 'other' hunter, SP = space web weavers, AM = ambush hunters, EN = endangered, VU = vulnerable, LC = least concern.

Species	Guild	Family	Conservation Status	Acid Grassland	Calcareous Grassland	Heath
Agroeca proxima	GH	Liocranidae	LC	6	14	17
Agyneta cauta	SW	Linyphiidae	LC	8	43	24
Agyneta conigera	SW	Linyphiidae	LC	6	26	10
Agyneta decora	SW	Linyphiidae	LC	51	11	42
Agyneta olivacea	SW	Linyphiidae	LC	2	2	0
Agyneta ramosa	SW	Linyphiidae	LC	0	0	1
Agyneta subtilis	SW	Linyphiidae	VU	19	91	164
Allomengea scopigera	SW	Linyphiidae	VU	0	0	3
Alopecosa pulverulenta	GH	Lycosidae	LC	57	28	32
Bathyphantes gracilis	SW	Linyphiidae	LC	5	2	1
Bathyphantes parvulus	SW	Linyphiidae	LC	0	3	1
Bolyphantes luteolus	SW	Linyphiidae	LC	0	3	1
Centromerita concinna	SW	Linyphiidae	LC	12	19	6
Centromerus dilutus	SW	Linyphiidae	LC	10	3	13
Centromerus prudens	SW	Linyphiidae	LC	9	5	8
Ceratinella brevipes	SW	Linyphiidae	LC	3	8	59
Ceratinella brevis	SW	Linyphiidae	LC	0	1	0

Clubiona diversa	O	Clubionidae	LC	3	6	3
Clubiona trivialis	O	Clubionidae	LC	0	0	1
Cnephalocotes obscurus	SW	Linyphiidae	LC	4	0	1
Coelotes atropos	SW	Agelenidae	LC	8	19	0
Dicymbium tibiale	SW	Linyphiidae	LC	7	21	35
Diplocentria bidentata	SW	Linyphiidae	LC	0	0	1
Diplocephalus latifrons	SW	Linyphiidae	LC	0	1	0
Dismodicus bifrons	SW	Linyphiidae	LC	3	0	4
Drassodes cupreus	GH	Gnaphosidae	LC	3	4	0
Erigone atra	O	Linyphiidae	LC	0	1	0
Erigone dentipalpis	O	Linyphiidae	LC	0	3	0
Erigonella hiemalis	O	Linyphiidae	LC	7	5	3
Gonatium rubellum	SW	Linyphiidae	LC	0	0	1
Gonatium rubens	SW	Linyphiidae	LC	9	8	9
Gongylidiellum vivum	SW	Linyphiidae	LC	44	0	27
Hahnia montana	SW	Hahniidae	LC	6	6	1
Hahnia nava	SW	Hahniidae	LC	2	22	3
Haplodrassus signifer	GH	Gnaphosidae	LC	13	8	0
Hypomma bituberculatum	SW	Linyphiidae	LC	7	4	8
Jacksonella falconeri	SW	Linyphiidae	EN	2	13	2
Semljicola faustus	SW	Linyphiidae	LC	0	0	5
Tenuiphantes cristatus	SW	Linyphiidae	LC	1	1	0
Palliduphantes ericaeus	SW	Linyphiidae	LC	155	190	269
Palliduphantes insignis	SW	Linyphiidae	LC	1	1	1
Tenuiphantes mengei	SW	Linyphiidae	LC	174	209	184
Tenuiphantes tenebricola	SW	Linyphiidae	LC	0	2	0
Tenuiphantes tenuis	SW	Linyphiidae	LC	0	6	2

Tenuiphantes zimmermanni	SW	Linyphiidae	LC	3	4	128
Agyneta affinis	SW	Linyphiidae	LC	4	13	0
Agyneta saxatilis	SW	Linyphiidae	LC	3	0	0
Micrargus herbigradus	SW	Linyphiidae	LC	77	24	26
Micrargus subaequalis	SW	Linyphiidae	LC	0	3	0
Monocephalus fuscipes	SW	Linyphiidae	LC	12	29	51
Oedothorax apicatus	O	Linyphiidae	LC	1	1	0
Oedothorax fuscus	O	Linyphiidae	LC	4	1	0
Oedothorax gibbosus	O	Linyphiidae	LC	5	2	2
Oedothorax retusus	O	Linyphiidae	LC	69	32	6
Ozyptila antomaria	AM	Thomisidae	LC	3	3	0
Ozyptila trux	AM	Thomisidae	LC	1	2	0
Pachygnatha degeeri	OW	Tetragnathidae	LC	613	324	121
Pardosa nigriceps	GH	Lycosidae	LC	13	22	58
Pardosa palustris	GH	Lycosidae	LC	2	45	5
Pardosa prativaga	GH	Lycosidae	LC	0	1	0
Pardosa pullata	GH	Lycosidae	LC	889	774	157
Pelecopsis mengei	SW	Linyphiidae	LC	16	1	101
Peponocranium ludicrum	SW	Linyphiidae	LC	15	14	55
Pholcomma gibbum	SW	Linyphiidae	LC	1	1	2
Pirata piraticus	SW	Lycosidae	LC	1	0	0
Pocadicnemis pumila	SW	Linyphiidae	LC	144	264	107
Poeciloneta variegata	SW	Linyphiidae	LC	1	1	0
Porrhomma egeria	SW	Linyphiidae	EN	0	0	2
Porrhomma montanum	SW	Linyphiidae	LC	1	0	4
Porrhomma pallidum	SW	Linyphiidae	LC	0	0	1
Robertus lividus	SP	Theridiidae	LC	36	11	49

Saaristoa abnormis	SW	Linyphiidae	LC	29	26	38
Savignia frontata	SW	Linyphiidae	LC	0	3	0
Silometopus elegans	SW	Linyphiidae	LC	318	441	127
Tapinocyba praecox	SW	Linyphiidae	LC	3	9	0
Textrix denticulata	SW	Linyphiidae	LC	0	0	1
Tiso vagans	SW	Linyphiidae	LC	41	167	0
Trichopternoides thorelli	SW	Linyphiidae	VU	2	0	0
Trochosa terricola	GH	Lycosidae	LC	108	158	39
Walckenaeria acuminata	SW	Linyphiidae	LC	17	13	45
Walckenaeria antica	SW	Linyphiidae	LC	91	73	22
Walckenaeria cuspidata	SW	Linyphiidae	LC	1	0	0
Walckenaeria dysderoides	SW	Linyphiidae	VU	0	2	2
Walckenaeria incisa	SW	Linyphiidae	VU	0	1	0
Walckenaeria monoceros	SW	Linyphiidae	VU	0	1	0
Walckenaeria nudipalpis	SW	Linyphiidae	LC	4	0	3
Walckenaeria vigilax	SW	Linyphiidae	LC	100	30	17
Xysticus cristatus	AM	Thomisidae	LC	14	29	3
Drassyllus pusillus	GH	Gnaphosidae	LC	1	1	0